

# RECORDS OF THE AUSTRALIAN MUSEUM

---

Volume 72

Number 3

29 July 2020

---

Eastern Australian land snail species  
closely related to *Austrochloritis porteri* (Cox, 1868),  
with description of a new species  
(Mollusca, Eupulmonata, Camaenidae)

*by*

Michael Shea and Frank Köhler

Neotype designation for the Australian Pig-footed Bandicoot  
*Chaeropus ecaudatus* Ogilby, 1838

*by*

Kenny J. Travouillon, Harry Parnaby and Sandy Ingleby

Ceriantharia (Cnidaria) from Australia, New Zealand  
and Antarctica with descriptions of four new species

*by*

Sérgio N. Stampar, V. Sadie Mills and Stephen J. Keable



## Editorial Board

Dr Shane Ah Yong, ICZN COMMISSIONER  
Dr Don Colgan  
Dr Mark Eldridge  
Dr Elena Kupriyanova  
Dr Andrew Mitchell  
Dr Amy Mosig Way  
Dr Robin Torrence

## Editor

Dr Shane McEvey



The works published by the Australian Museum in this issue are licensed under a Creative Commons Attribution 4.0 International License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original authors and source are credited.

Volume 72 Number 3

Published (print and online) 29 July 2020

Price: AU\$50.00

Printed by Roden Print & Packaging, Sydney

ISSN 0067-1975 (print)

ISSN 2201-4349 (online)

The Australian Museum is a statutory authority of, and principally funded by, the NSW State Government.



The Australian Museum houses some of the world's most important collections of Australian animal, fossil and geological specimens and cultural objects. Research on these millions of specimens and artefacts yields insights into how our world changes through time and how its diversity can be classified, interpreted, and appreciated. This knowledge, when shared among the scientific and broader community—initially through publication—helps us understand the significance of the impact we have on our environment. The collections represent key research infrastructure that will have increasingly significant value through the rest of this century and into the future. From this resource, we come to know what reasonable steps society can take now for the well-being of future generations. Our responsibility is also to inspire the exploration of nature and cultures; our vision is a beautiful and sustainable natural world with vibrant and diverse cultures that we are able to see, appreciate and know deeply.

Since 1827, the results of studies on Australian Museum collections, or studies that more generally lead to a better understanding of nature and cultures in Australia and the Pacific, have been published by the Museum. Our leading science journal, *Records of the Australian Museum*, was first published in 1889. In 1999 we began releasing PDF of published articles through our open access website. In 2008 we adopted DOI registration for our online content to facilitate persistence and cross-linking in the scientific literature. In 2009 we digitized, articalized and DOI-registered the entire legacy of all science published by us since 1851, and made that huge searchable resource permanently and freely available online. Since 2016 most authors are ORCID-registered. Since 2017 articles are ZooBank registered. PDF are externally archived at NED (Australia's *National edeposit*), and, from 2019, works are licensed under a Creative Commons Attribution 4.0 International License (CC BY 4.0). To accelerate publication of peer-reviewed science we adopted (from volume 65, 2014) a one- or several-article-per-issue model and we are limiting, but not abandoning, print production. There were five issues published in volume 70 (2018), seven in volume 71 (2019). All that is published in print is immediately and freely available online.

Authors are invited to submit manuscripts to the Editor. Manuscripts meeting subject and stylistic requirements outlined in the *Instructions to Authors* (see inside back cover) are peer-reviewed by external referees to meet standards of excellence set by the Editorial Board.

<https://doi.org/10.3853/issn.2201-4349>

*Records of the Australian Museum* is covered in the Thomson Reuters Scientific services: Current Contents® / Agriculture, Biology, and Environmental Sciences, and Science Citation Index Expanded (also known as SciSearch®)

We promote cross-linking in the scientific literature by using DOI for all Australian Museum scientific publications, article-by-article back to 1889; metadata in CrossRef® and, from 2017, also in ZooBank. PDF are externally archived at NED (Australia's *National edeposit*). Authors are ORCID® registered.

# Eastern Australian Land Snail Species Closely Related to *Austrochloritis porteri* (Cox, 1868), with Description of a New Species (Mollusca, Eupulmonata, Camaenidae)

MICHAEL SHEA  AND FRANK KÖHLER 

Australian Museum Research Institute,  
Australian Museum, 1 William Street, Sydney NSW 2010, Australia

**ABSTRACT.** The systematic taxonomy of three currently accepted species of *Austrochloritis* Pilsbry, 1891 from central eastern New South Wales (*A. mundinalis* Iredale, 1943, *A. niangala* Shea & Griffiths, 2010, and *A. kaputarensis* Stanisic, 2010) is revised based on comparative morpho-anatomy and mitochondrial phylogenetics. In addition, the status of two undescribed candidate taxa identified as *Austrochloritis* spp. NE3 and SN39, respectively, is assessed. These species and candidate species are closely related to the type species of the genus, *Austrochloritis porteri* (Cox, 1866) from southern Queensland based on a recently published mitochondrial phylogeny.

Comparative analyses of shell and reproductive anatomy revealed that the members of the *A. porteri* clade exhibit a rather similar morphology overall. Based on subtle, yet consistent differences in shell and reproductive features, we consider *A. mundinalis* as an accepted species. The species *A. niangala*, *A. kaputarensis*, and NE3 are considered as synonyms of each other and preference is given to the name *A. niangala* by First Reviewers Choice. The candidate taxon SN39 represents a new species, which is herein described as *Austrochloritis copelandensis* sp. nov.

## Introduction

*Austrochloritis* Pilsbry, 1891 is taxonomically a comparatively diverse, yet morphologically rather homogeneous land snail genus endemic to eastern Australia (e.g., Stanisic *et al.* 2010). *Austrochloritis* species, with a few exceptions, are overall similar externally, having rather small, depressed and ‘hairy’ shells of dull brown colour. Because of their similar nondescript appearance, most species are currently difficult to identify based on the classification system introduced by Stanisic *et al.* (2010), which relies exclusively on shell characters in combination with the documented or presumed distribution of species. Nearly all species, both currently accepted and unaccepted, are known only from their shells while taxonomically critical information

on their comparative anatomy is almost entirely lacking. Exceptionally, we recently described the reproductive anatomy of two species: *Austrochloritis porteri* (Cox, 1866), the type species of the genus, and *A. specularis* Shea & Griffiths, 2010, a species from the Northern Tablelands of New South Wales (Shea and Köhler 2019).

In addition, we scrutinized the current systematic classification by analysing the differentiation in mitochondrial DNA sequences (Köhler, Criscione, and Shea 2020). This study has revealed widespread incongruence between the current species-level classification and the branching patterns of the mitochondrial trees. Most significantly, we found that many species as currently delineated were non-monophyletic in the phylogenetic trees. This incongruence may be attributed to a wide range

**Keywords:** Gastropoda; mitochondrial DNA; reproductive anatomy; shell morphology; New South Wales

**Zoobank registration:** urn:lsid:zoobank.org:pub:9585ACBD-83D7-4292-B804-1313B911BD88

**Corresponding author:** Frank Köhler [frank.koehler@austmus.gov.au](mailto:frank.koehler@austmus.gov.au)

**Received:** 15 November 2019 **Accepted:** 3 June 2020 **Published:** 29 July 2020 (in print and online simultaneously)

**Publisher:** The Australian Museum, Sydney, Australia (a statutory authority of, and principally funded by, the NSW State Government)

**Citation:** Shea, Michael, and Frank Köhler. 2020. Eastern Australian land snail species closely related to *Austrochloritis porteri* (Cox, 1868), with description of a new species (Mollusca, Eupulmonata, Camaenidae). *Records of the Australian Museum* 72(3): 63–76. <https://doi.org/10.3853/j.2201-4349.72.2020.1759>

**Copyright:** © 2020 Shea, Köhler. This is an open access article licensed under a Creative Commons Attribution 4.0 International License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original authors and source are credited.



of potential problems relating to the systematic significance of available morphological and molecular evidence. For example, the sole reliance of the current classification on shell characters is problematic because shell features may be homoplastic due to their potentially adaptive nature. It is well-documented that shell characteristics may be conserved in species pursuing identical life styles while living in similar environments as the result of balancing selection. Such morphological conservatism may lead to an underestimation of the true taxonomic diversity in morphologically conserved groups as was demonstrated for the northern Australian camaenid *Mesodontrachia* by Criscione & Köhler (2013). On the other hand, shell characters may also be polymorphic within species that inhabit heterogeneous environments, which may lead to an overestimation of taxonomic diversity (e.g., Davison & Clarke, 2000; Criscione & Köhler, 2016a).

However, the mitochondrial markers underpinning our previous phylogenetic hypothesis are not without potential caveats either as several mechanisms may cause the non-monophyly of species in mtDNA trees, such as paralogy, retention of ancestral polymorphisms, or introgressive hybridization, to name just a few (e.g., Funk & Omland, 2003; Ballard & Whitlock, 2004). Indeed, there are several well-documented cases in which mtDNA markers proved to be unreliable for the delineation of species, especially in cerithioidean freshwater snails (e.g., Köhler & Deen, 2010; Köhler, 2016, 2017; Whelan & Strong, 2016). However, mtDNA has so far appeared as a reliable source of systematic information in a wide range of Australian camaenids (e.g., O'Neill *et al.*, 2014; Criscione & Köhler, 2014a,b, 2016b; Taylor *et al.*, 2015; Johnson *et al.*, 2016; Köhler & Burghardt, 2016).

Putting the difficulties with species delineation aside, our molecular phylogenetic study has highlighted the importance of the Hunter Valley as an effective biogeographic barrier separating temperate and subtropical species of *Austrochloritis*. Species on either side of this divide revealed remarkably different biogeographic patterns: One of widespread parapatry of species south of the Hunter Valley and of potentially widespread sympatry north of it. Usually, species occurring in sympatry with each other were found not to belong to closely related main clades in the phylogenetic tree.

Based on the observation of widespread sympatry of possibly morphologically cryptic species north of the Hunter Valley, we also consider the existence of undescribed, morphologically rather cryptic species, as another possible explanation for the observed incongruence between molecular phylogeny and morphological species delineation. Hence, to resolve the prevailing ambiguity in the delineation of *Austrochloritis* species, it is critical to base any systematic appraisal on more comprehensive evidence, such as previously ignored morpho-anatomical and genetic data. In addition, increasing the number of studied specimens and populations should be useful to improve our understanding of the amounts of variation within and between species especially in cases where sympatry of morphologically cryptic species has been postulated (Köhler *et al.*, 2020).

Our mitochondrial phylogenies (Köhler *et al.*, 2020) contained several well-differentiated and well-supported main clades (clades A–E), which are postulated to represent well-differentiated species or species groups within *Austrochloritis*. One of these clades, Clade B, contained

sequences of the type species, *A. porteri* (Cox, 1868), three additional nominal species (*A. mundinalis* Iredale, 1943, *A. niangala* Shea & Griffiths, 2010, *A. kaputarensis* Stanisc, 2010), and two supposedly undescribed species (*Austrochloritis* sp. NE3 and SN39). Each of these taxa or candidate taxa was represented by just two sequences and one of them, *A. niangala*, was found not to be monophyletic.

In the present study, we assess the variation in shell and reproductive anatomy among representatives of this clade in combination with a slightly increased sampling of mitochondrial DNA sequences in order to more objectively delimit distinct species.

## Materials and methods

This study is based on examination of all relevant samples housed in the collections of the Australian Museum, Sydney (AM), including historic and newly collected material, both wet and dry. A Leica MZ8 stereo microscope with a drawing apparatus was used to examine the reproductive anatomy of ethanol preserved samples by means of anatomical dissection. Bodies were removed from shells prior to dissection and shells were photographed. Shell height (H) and width (W) were measured with callipers accurate to 0.5 mm. We also counted the number of whorls (N) as shown by Köhler (2011). Selected shells were cleaned by gently brushing in warm soapy water, dried, mounted on carbon specimen tabs, and coated with gold for scanning electron microscopy.

DNA was extracted from small pieces of foot muscle by use of a QIAGEN DNA extraction kit for animal tissue following the standard procedure of the manual. Fragments of two mitochondrial genes, 16S rRNA (16S) and cytochrome c oxidase subunit 1 (COI) were amplified by PCR using the primer pairs 16Scs1 (Chiba 1999) and 16Sbd1 (Sutcharit, Asami, and Panha 2007) and L1490 and H2198 (Folmer *et al.* 1994), respectively. Reactions were performed with an annealing step of 60 s at 55°C for 16S and at 50°C for COI with elongation times of 60–90 s respectively. Both strands of PCR fragments were purified with ExoSAP (Affymetrix) and cycle sequenced by use of the PCR primers. Chromatograms were manually corrected for misreads, if necessary, and forward and reverse strands were merged into one contig using CodonCode Aligner v. 3.6.1 (CodonCode Corporation, Dedham, MA). New sequences have been deposited in GenBank. The 16S sequences were aligned using the online version of MAFFT (version 7.4) (Katoh *et al.*, 2002) available at <http://mafft.cbrc.jp/alignment/server/> by employing the iterative refinement method E-INS-i. We used the online version of Gblocks (Version 0.91b) (Castresana, 2000) to identify and remove unreliable alignment regions in the 16S alignment by employing options for a less stringent selection. The final sequence alignments of 16S and COI were concatenated into one partitioned data set. Four partitions were designated: The entire 16S fragment plus each of the three codon positions of the COI fragment. The best-fit model of nucleotide substitution was identified for each sequence partition separately using ModelFinder included in IQ-Tree (Kalyaanamoorthy *et al.*, 2017). Phylogenetic relationships were estimated by employing a Maximum Likelihood-based method of tree reconstruction using the program IQ-Tree (Nguyen *et al.*, 2015). Nodal

support of the best ML tree was estimated by performing 10,000 ultrafast bootstraps in IQ-Tree (Minh *et al.*, 2013).

Our operational criterion for the delimitation of species was to test whether candidate species were phenotypically distinct from each other (Sites & Marshall, 2004). Candidate taxa were initially delimited by grouping specimens in accordance with their shell morphology with reference to the current taxonomy. In a second step we assessed if these groups can be confirmed as consistently distinct groups with respect to their comparative reproductive anatomy and if they are recovered as monophyletic clusters in the mitochondrial phylogeny. We also employed basic statistics of morphometric characters to assess the morphometric similarity or distinctiveness of the candidate taxa. Candidate taxa that could be distinguished consistent by comparative morpho-anatomy and are also well-differentiated from each other in the mtDNA tree, were accepted as distinct species. Candidate species that could not be consistently distinguished from each other were lumped together.

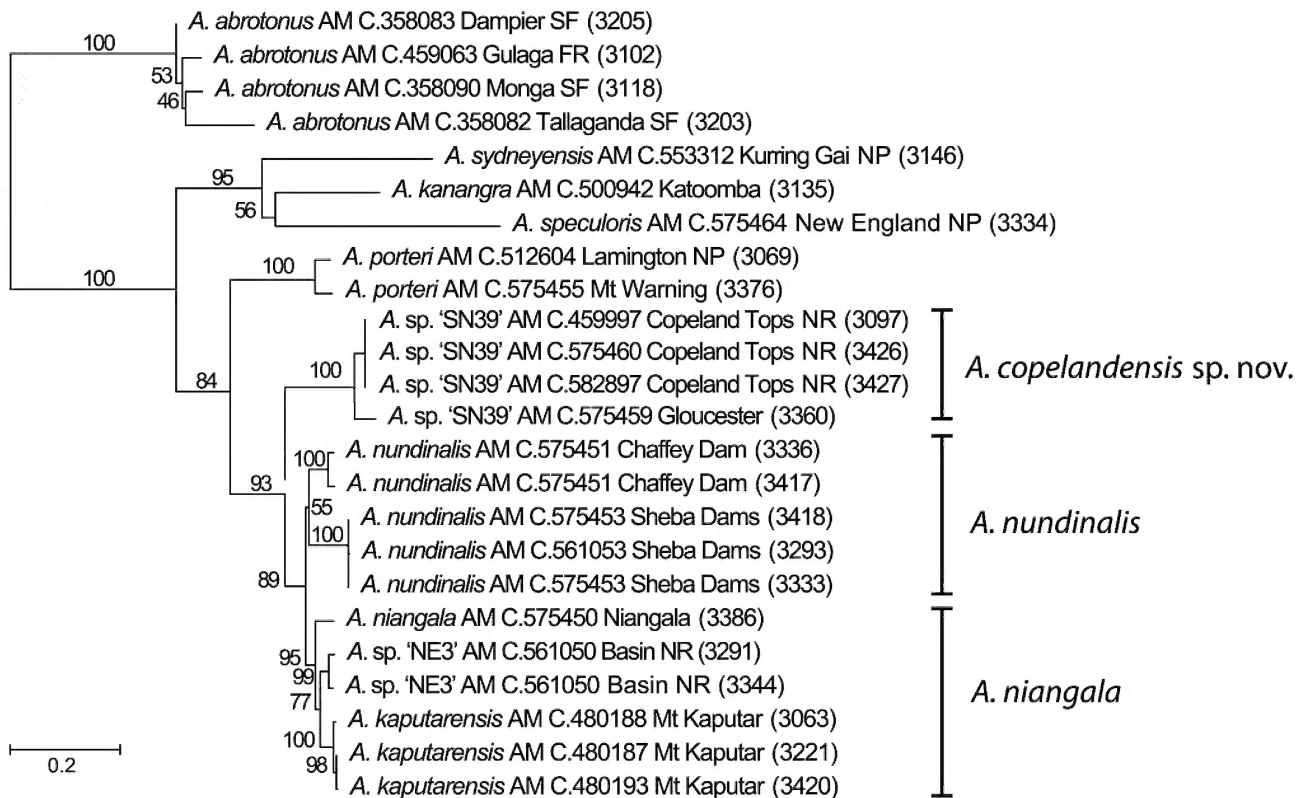
**Abbreviations.** *Morpho-anatomy*: *at*, atrium; *ag*, albumen gland; *bc*, bursa copulatrix; *bh*, head of bursa copulatrix; *d*, number of dry shells per lot; *ep*, epiphallus; *fl*, flagellum; *H*, height of shell; *N*, number of whorls; *p*, penis; *pv*, penial verge; *pw*, penial wall; *rm*, penial retractor muscle; *so*, spermoduct; *va*, vagina; *vd*, vas deferens; *w*, number of preserved specimens per lot; *W*, width of shell. *Geographic*: *HS*, homestead; *NP*, National Park; *NR*, Nature Reserve; *NSW*, New South Wales.

## Results

### Mitochondrial phylogenetics

We constructed a DNA sequence dataset by concatenating partial sequences of the mitochondrial genes cytochrome *c* oxidase subunit 1 (COI) and 16S rRNA (16S). The final dataset contained sequences of 24 individuals (four of *A. mundinalis*, three of *A. kaputarensis*, one of *A. niangala*, three of *Austrochloritis* sp. NE3, four of *Austrochloritis* sp. SN39, as well as seven sequences of other *Austrochloritis* species that were used as outgroup to root the tree). This sampling included sequences of topotypic specimens of *A. kaputarensis* and *A. niangala*, the holotype and paratype of the newly described species, and material from close to the type locality of *A. mundinalis* (i.e., from Sheba Dam).

In this dataset three COI sequences of in-group taxa were missing whereas the 16S sequences were completely sampled. All COI sequences had a length of 655 bp after pruning of the primer sites while the multiple 16S sequence alignment had a length of 782 bp after trimming of ends and removing ambiguously aligned sections by using Gblocks. For the phylogenetic analysis a data partition was applied, which allowed parameters for each codon position of the COI fragment and the 16S fragment to be modelled independently. The model test implemented in IQ-Tree identified the following models of sequence evolution as the best-fit models for the different partitions by means of the Bayesian Information Criterion: TVM+F+I+G for 16S,



**Figure 1.** Bootstrap consensus tree for 10,000 ultrafast Maximum Likelihood bootstraps as based on Maximum Likelihood Analysis of the concatenated 16S and COI sequence dataset. Sequences of *Austrochloritis abrotonus* Shea & Griffiths, 2010 were used to root the tree.

F81+F+I for 1st, TIM+F+G for 2nd, and TN+F+G for 3rd codon positions in COI. These models were applied in the partitioned Maximum Likelihood analysis.

The bootstrap consensus tree of the Maximum Likelihood Analysis confirmed *A. porteri* as the sister group to the in-group consisting of *A. mundinalis*, *A. niangala*, *A. kaputarensis* as well as the candidate species *A. sp. NE3* and *A. sp. SN39* with good statistical support (Fig. 1). All nominal and candidate species formed monophyletic clusters. However, the bootstrap support for the monophyly of *A. mundinalis* was low as individuals from two distinct locations formed two well-differentiated sub-clades. The taxa *A. kaputarensis*, *A. niangala* and *Austrochloritis sp. NE3* together formed a clade with comparatively short internal branches. The maximum uncorrected pairwise distances in 16S were low within this clade: 1.1 % among three sequences of *A. kaputarensis* and 1.5 % between two sequences of *Austrochloritis sp. NE3*. However, the maximum pairwise distance between all sequences of this clade was 4.3 % (for six sequences), which was comparable with the maximal p-distance of 6.7 % among the five sequences of *A. mundinalis* and the distance between the two sequences of *Austrochloritis sp. SN39*: 3.2 %.

### Comparative morpho-anatomy

All examined nominal and candidate species are characterized by exhibiting a largely similar shell morphology and reproductive anatomy. However, some minor, yet consistent differences exist.

We found that *A. niangala*, *A. kaputarensis*, and *A. sp. NE3* were effectively indistinguishable in both shell morphology (shell size, shape, periostracal projections, sculpture, coloration) and reproductive anatomy (anatomical detail, relative lengths of penis, epiphallus, penial verge, and bursa copulatrix, development of flagellum, bursa head, penial pilasters).

*Austrochloritis mundinalis* exhibited a very similar reproductive anatomy compared to the above-mentioned taxa. However, it could be distinguished from them by its significantly larger shell and by a different shape of the periostracal projections covering its shell (curved instead of straight).

*Austrochloritis sp. SN39* had a very similar shell compared to *A. mundinalis* in terms of shape and size. However, it differed from all other taxa by having a well-reflected aperture and a much longer and pointed penial verge.

## Systematics

Family Camaenidae Pilsbry, 1895

### Genus *Austrochloritis* Pilsbry, 1891

**Type species:** *Helix porteri* Cox, 1866, by original designation. For diagnosis and taxonomic details refer to Stanisc *et al.* (2010) and Shea & Köhler (2019).

### *Austrochloritis mundinalis* Iredale, 1943

*Austrochloritis mundinalis* Iredale, 1943: 64 (probable syntypes AM C.112312, 2d, from Nundle, NSW); Stanisc *et al.*, 2010: 384, fig. 570.

**Type material examined.** Probable syntypes, AM C.112312 (2 d; Nundle) (Fig. 2A).

**Non-type material examined:** AM C.171350 (3 d; Ponderosa Forest Park, Nundle SF, E of Nundle, -31.47° 151.26°; alt. 1,250 m; eucalypt forest), AM C.171513 (9 d; Sheba Dams, 14 km SE of Nundle, -31.498° 151.195°; tall, moist eucalypt forest), AM C.335318 (1 d; 5 km ESE of Nundle, -31.48° 151.18°), AM C.339647 (4 d; Chaffey Dam, NW end of wall, S of Woolomin, -31.345° 151.135°; open eucalypt woodland), AM C.459889 (1 d; Nundle SF, -31.48° 151.37°; sclerophyll forest), AM C.459901 (4 d; same as AM C.459889), AM C.575259 (15 d; E side of Chaffey Dam, 5 km N of Bowling Alley Point, -31.37° 151.14°; alt. 550 m; dry sclerophyll woodland), AM C.575451 (3 w; same as AM C.575259); AM C.575260 (2 d; Sheba Dams camping area, east of Nundle, -31.50° 151.20°; alt. 1,173 m; moist sclerophyll forest), AM C.575453 (3 w; same as AM C.575260).

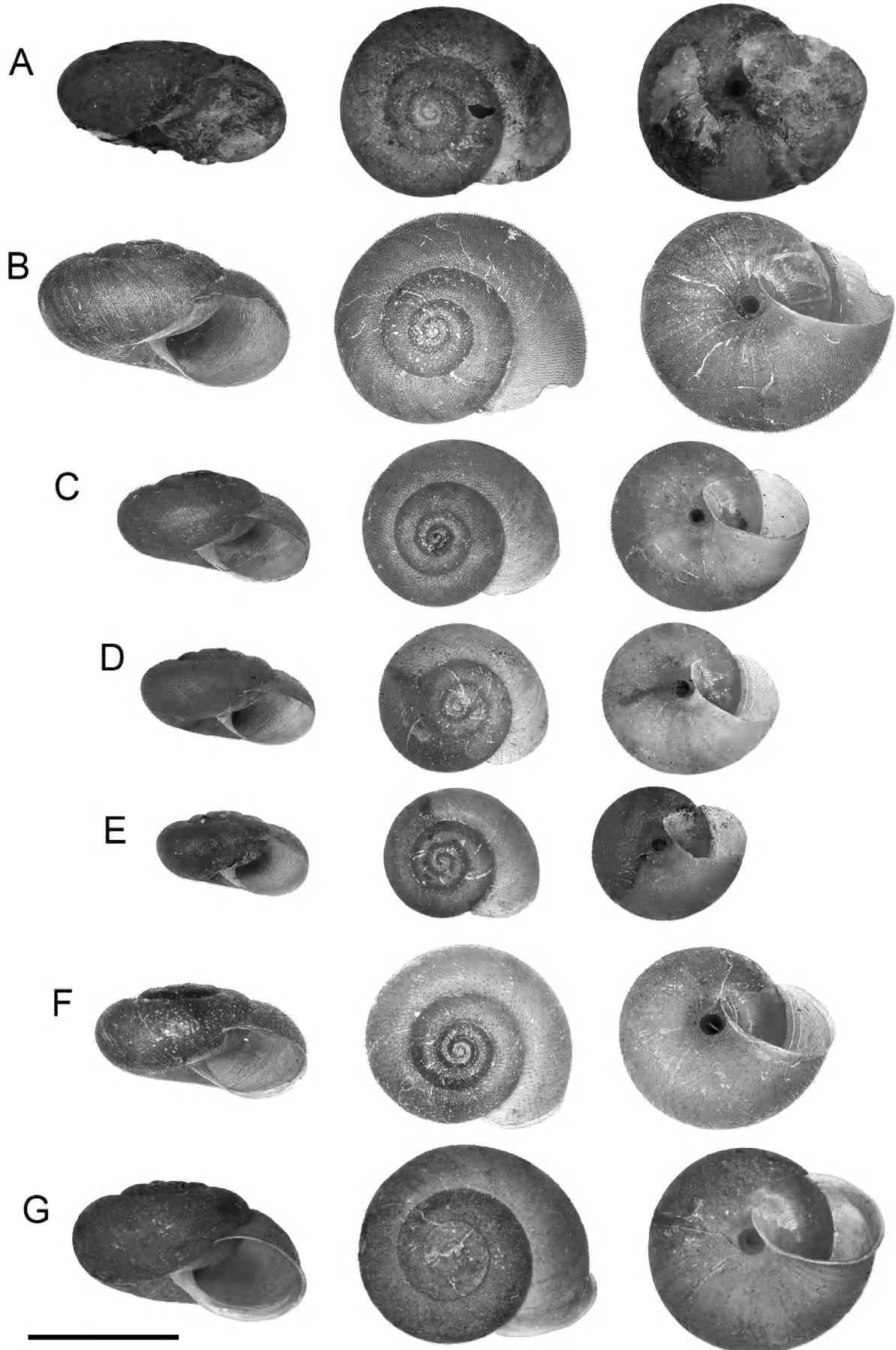
### Taxonomic remarks

The original description is rather uninformative, stating that this species is similar to *A. porteri*, but differs by its higher spire and denser hair (Iredale, 1943: 64). Iredale's description does not contain an explicit type designation. Subsequently, Stanisc *et al.* (2010: 384) stated that *A. mundinalis* was "distinguished [from other congeners] by combination of relatively large size, flattened spire, fine moderately long setae and weakly reflected lip".

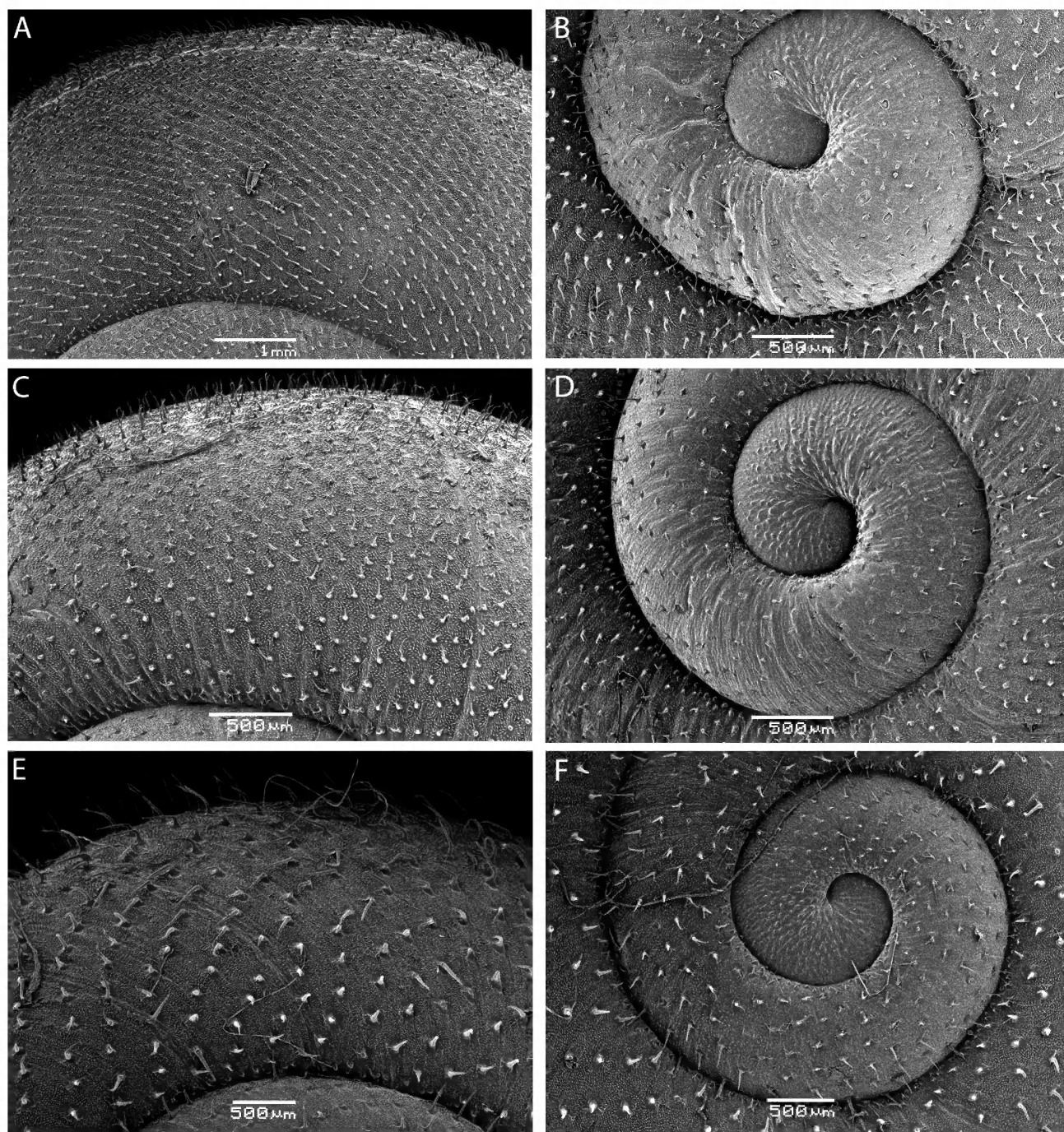
**Table 1.** Shell dimensions (*H*=height, *W*=width, *N*=number of whorls) of mature shells of *Austrochloritis mundinalis*, *A. niangala* and *A. copelandensis* sp. nov.

|                                  |          | H          | W           | N         |
|----------------------------------|----------|------------|-------------|-----------|
| <i>A. mundinalis</i>             |          | 9.3        | 15.7        | 3.5       |
|                                  | (n = 19) | (7.7–11.3) | (13.8–17.3) | (3.3–3.6) |
| <i>A. niangala</i>               |          | 7.4        | 12.7        | 3.5       |
|                                  | (n = 20) | (6.2–8.8)  | (11.1–15.0) | (3.2–3.9) |
| <i>A. copelandensis</i> sp. nov. |          | 9.0        | 16.1        | 4.1       |
|                                  | (n = 2)  | (8.9–9.0)  | (15.8–16.3) | (4.1–4.2) |





**Figure 2.** Shells (front, top, and umbilical view). (A, B) *Austrochloritis nundinalis*: A, probable syntype AM C.112312 (Nundle, NSW); B, AM C.575260 (Sheba Dams, E of Nundle); (C–F) *Austrochloritis niangala*: C, holotype, AM C.339934 (ESE of Tamworth); D, paratype of *A. kaputarensis*, AM C.452038 (NE of Manilla); E, AM C.478658 (Mt Kaputar); F, AM C.561050 (Georges Mountain, Basin NR); G, *Austrochloritis copelandensis* sp. nov., holotype AM C.582897 (Copeland Tops). Scale bar = 10 mm.



**Figure 3.** Scanning electron micrographs of shells of *Austrochloritis* (teleoconch viewed from above, protoconch viewed from above). (A, B) *Austrochloritis nundinalis*, AM C.171513, Nundle; (C, D) *A. niangala*, AM C.339933, Niangala; (E, F) *Austrochloritis* sp. NE3, AM C.561050). Scale bars: A = 1 mm, B–F = 0.5 mm.

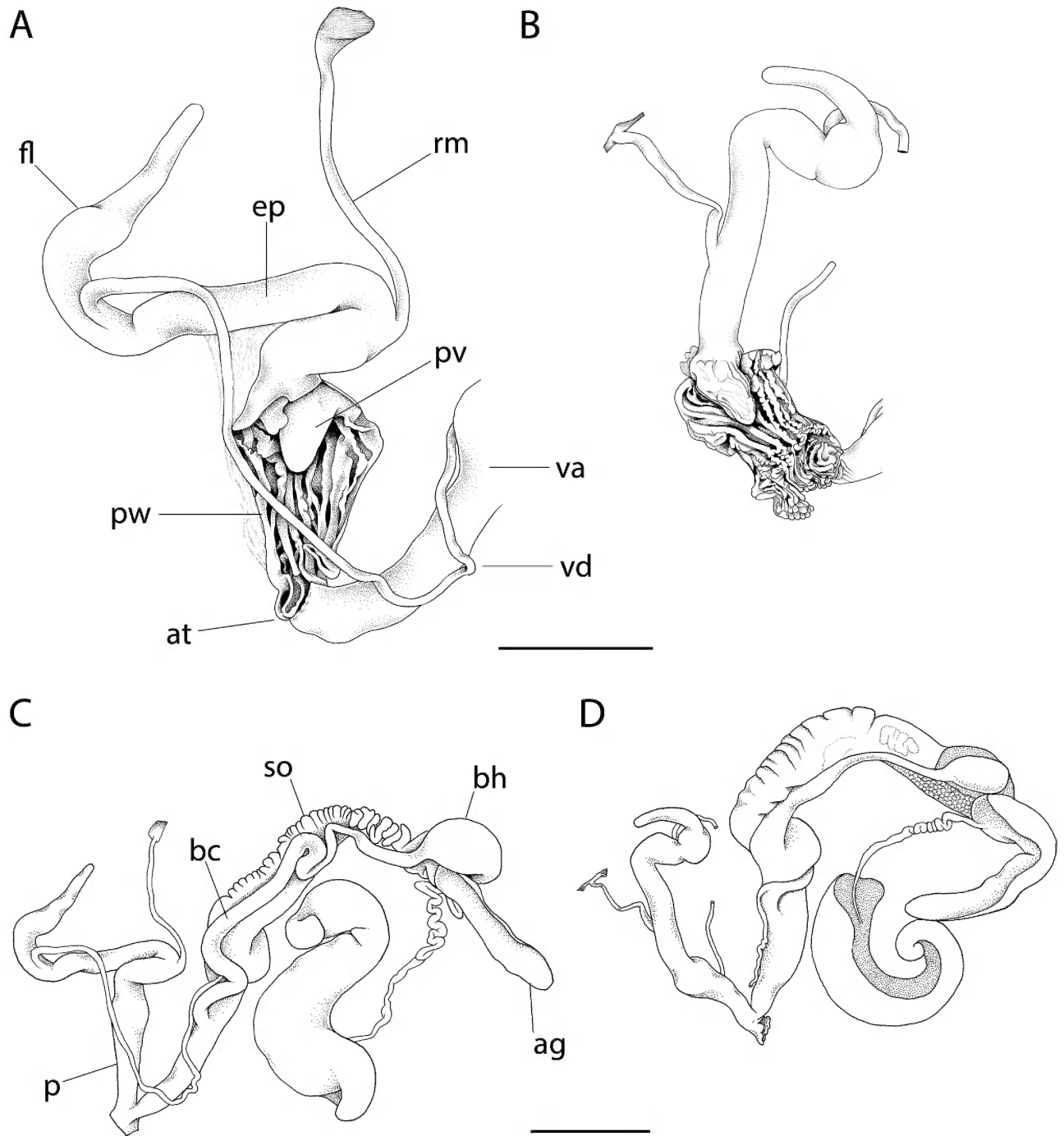
### Description

**Shell** (Figs 2A,B, 3A,B). Medium sized (W=13.8–17.3 mm, H=7.7–11.3 mm, N = 3.3–3.5; for n = 19; Table 1), depressedly subglobose, whorls rounded to slightly shouldered in cross-section, gradually increasing in diameter, suture moderately incised; protoconch sculpture of rugose radials with coarse pustules at apex, periostracal setae extending well onto protoconch; teleoconch sculpture of low growth lines and corrugations with periostracal sculpture of curved, crowded, short setae; interstitial microsculpture of very fine wavy periostracal ridgelets and scales; last whorl

strongly descending behind aperture in mature individuals; aperture moderately tilted forward from axis of coiling, without thickened or reflected outer lip and without sulcus behind lip; umbilicus narrowly open with U-shaped profile; shell colour pale yellowish to dark reddish brown.

**Reproductive anatomy** (Fig. 4). Penis cylindrical, without penial sheath, inner penial wall sculpture of many well-developed longitudinal pilasters, epiphallus about two to three times longer than penis, with well-developed finger-like epiphallic flagellum at distal end, about as long as penis; epiphallus communicates with penis through broadly conical,



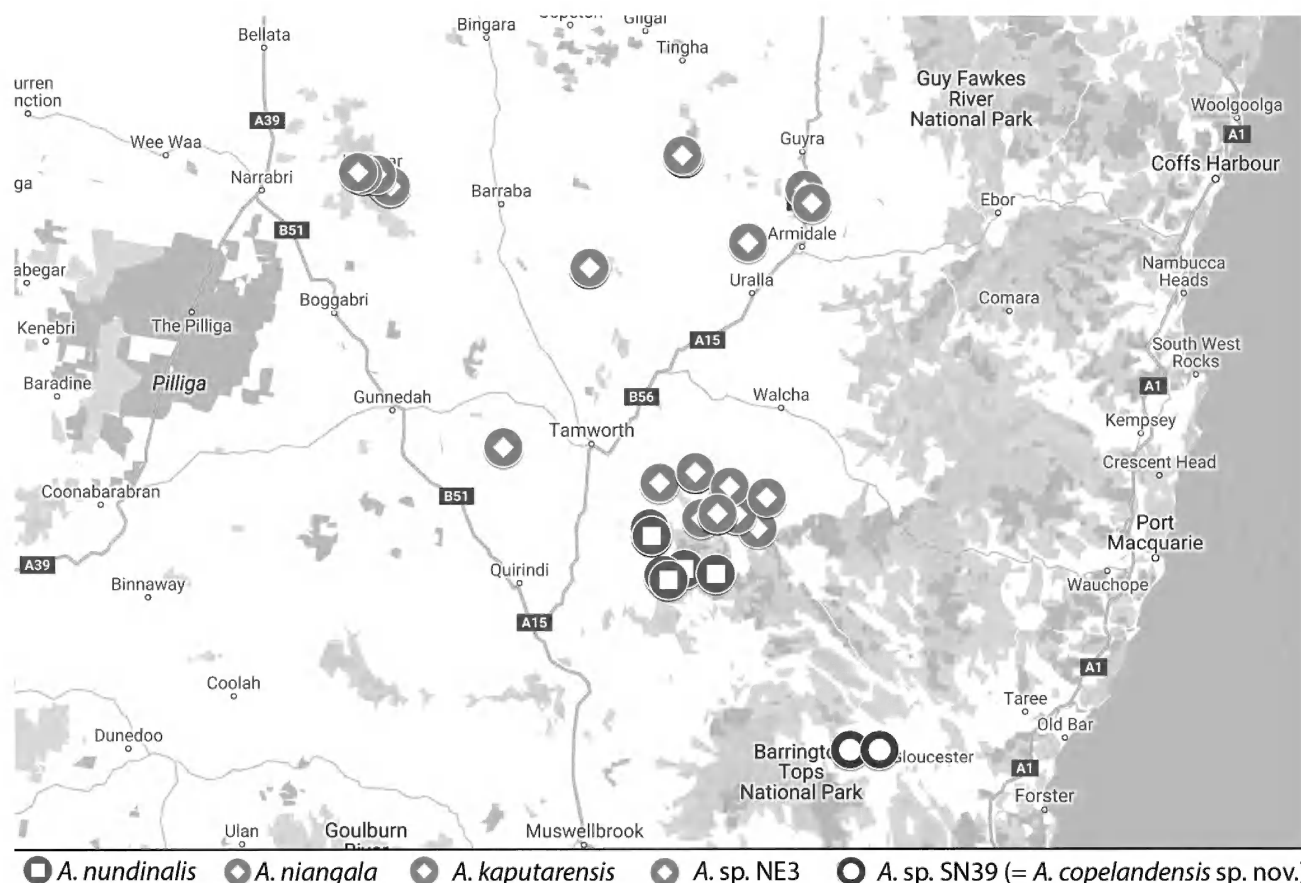


**Figure 4.** Reproductive anatomy of *Austrochloritis nundinalis*. (A) Penial anatomy, AM C.575453, Sheba Dams, E of Nundle; (B) penial anatomy, AM C.575451, Chaffey Dam; scale bar = 3 mm. (C) Reproductive system, AM C.575453, Sheba Dams, E of Nundle; (D) reproductive system, AM C.575451, Chaffey Dam; scale bar = 5 mm.

free penial verge, penial verge comprising about half to one third of penis length; penial retractor muscle attached to distal third of epiphallus, vas deferens entering head of epiphallus through single pore just below base of epiphallic flagellum; vagina cylindrical, about as long as penis, inner wall with prominent longitudinal pilasters; bursa copulatrix long, tubular with inflated bulb-like head, about as long as oviduct to one quarter longer, head reaching base of albumen gland; hermaphroditic duct inserting into head of talon (based on three dissected specimens).

### Comparative remarks

Reproductive morphology was variable among dissected specimens even within a single population: Penial length varied from about as long as vagina to half of vaginal length and the bursa copulatrix varied in length from about equivalent to the oviduct to substantially longer. The lack of a reflected outer lip and sulcus and setae extending well onto the protoconch distinguish this species from most other congeners. *Austrochloritis nundinalis* differs from *A. porteri*



**Figure 5.** Occurrence records of *Austrochloritis nundinalis*, *A. niangala* (= *A. niangala*, *A. kaputarensis*, *Austrochloritis* sp. NE3), and *A. copelandensis* sp. nov. (= *Austrochloritis* sp. SN39) from the malacological collection of the Australian Museum. Source of base map: Google Maps.

most notably in having a proportionally longer epiphallus, a different penial verge morphology (conical, smooth vs. elongated, sculptured), and a wider flagellum (Shea & Köhler, 2019). In addition, *A. nundinalis* has a significantly smaller shell. For a comparison with *A. niangala* refer below.

### Distribution and ecology

*Austrochloritis nundinalis* is so far only known from near Nundle, where it is mainly found at altitudes between 550–1,418 m (Fig. 5). It is found in sclerophyll forests, on granitic and basaltic bedrock; under logs, rocks and shed bark around base of trees. It seals to the underside of substrates with a tough parchment-like epiphragm in dry conditions.

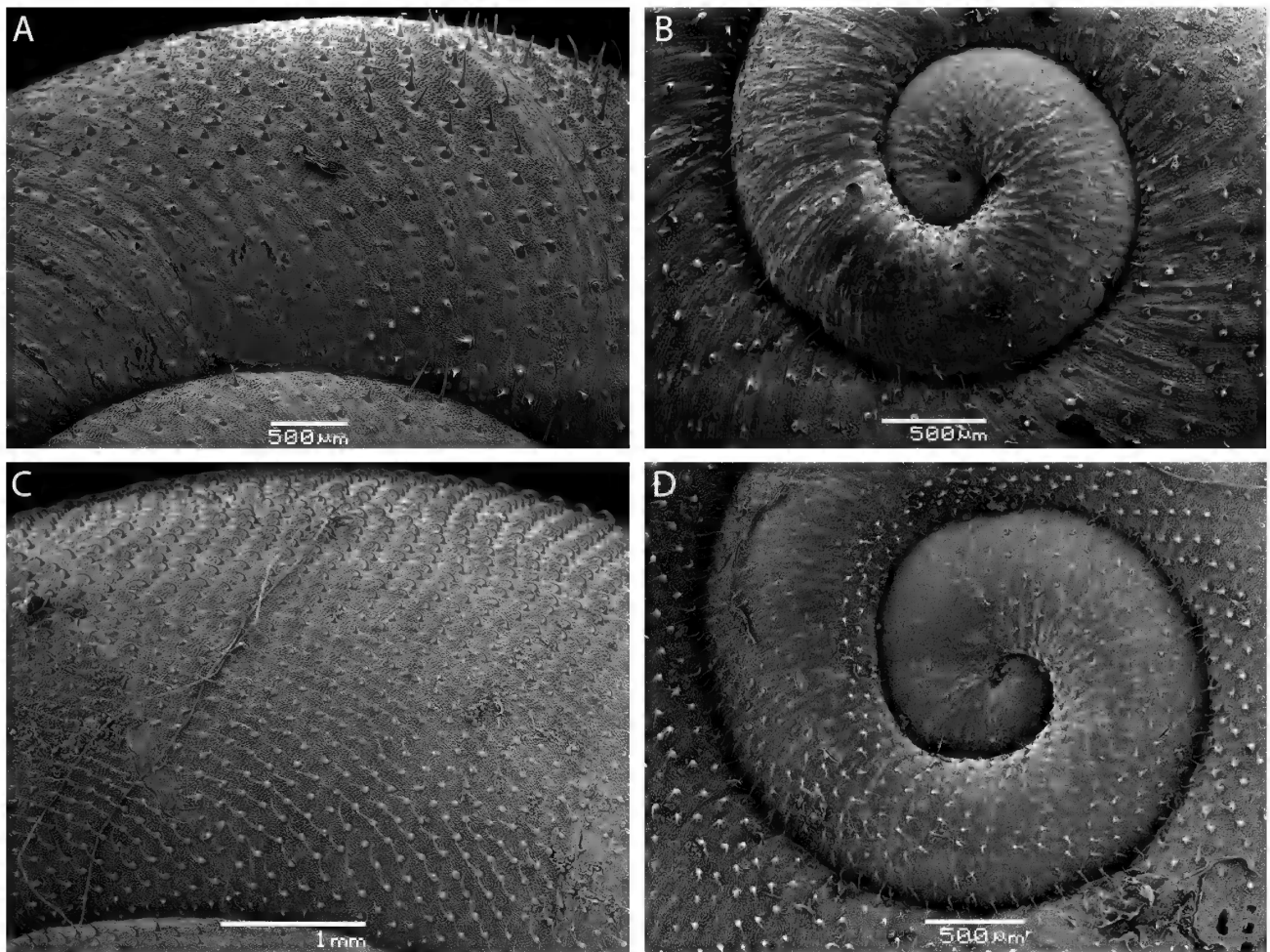
### *Austrochloritis niangala* Shea & Griffiths, 2010

*Austrochloritis niangala* Shea & Griffiths, 2010 in Stanisc, Shea, Potter & Griffiths, 2010: 384–385, 536 (holotype AM C.339934 from ESE of Tamworth, NE New South Wales, -31.177° 151.295°).

*Austrochloritis kaputarensis* Stanisc, 2010 in Stanisc, Shea, Potter & Griffiths, 2010: 384–385, 536 (holotype QM MO32626 from Dawson Spring, Mt Kaputar, -30.267° 150.167°); **new synonym**.

**Type material examined.** Holotype of *Austrochloritis niangala*, AM C.339934 (1 d, ESE of Tamworth, -31.177° 151.295°) (Fig. 2C), Paratypes, AM C.339935 (1 d, same as holotype), AM C.339933 (3 d, SE of Tamworth, near Three Corner Swamp, 300 m E of “Carnegie” HS). Paratypes of *Austrochloritis kaputarensis*, AM C.450448 (8 d, NE of Manilla, Warrabah NP, -30.267° 150.167°), AM C.452038 (1 d, same as AM C.450448).

**Non-type material examined.** AM C.339566 (1 w, ESE of Tamworth, 3.4 km E of Niangala, -31.30° 151.44°), AM C.339936 (1 d, 40 km S of Walcha, -31.34° 151.51°), AM C.446747 (1 d, Oakey Creek Nature Reserve, -31.10° 150.62°), AM C.339817 (1 w, 32 km SE of Kootingal, -31.21° 151.17°), AM C.108379 (1 w, 3.4 km E of Niangala, -31.30° 151.44°), AM C.339816 (2 w, same as holotype), AM C.478245 (7 d, same as holotype), AM C.339928 (2 w, S of Walcha, Ingleba Ck, N of Branga Plains HS,

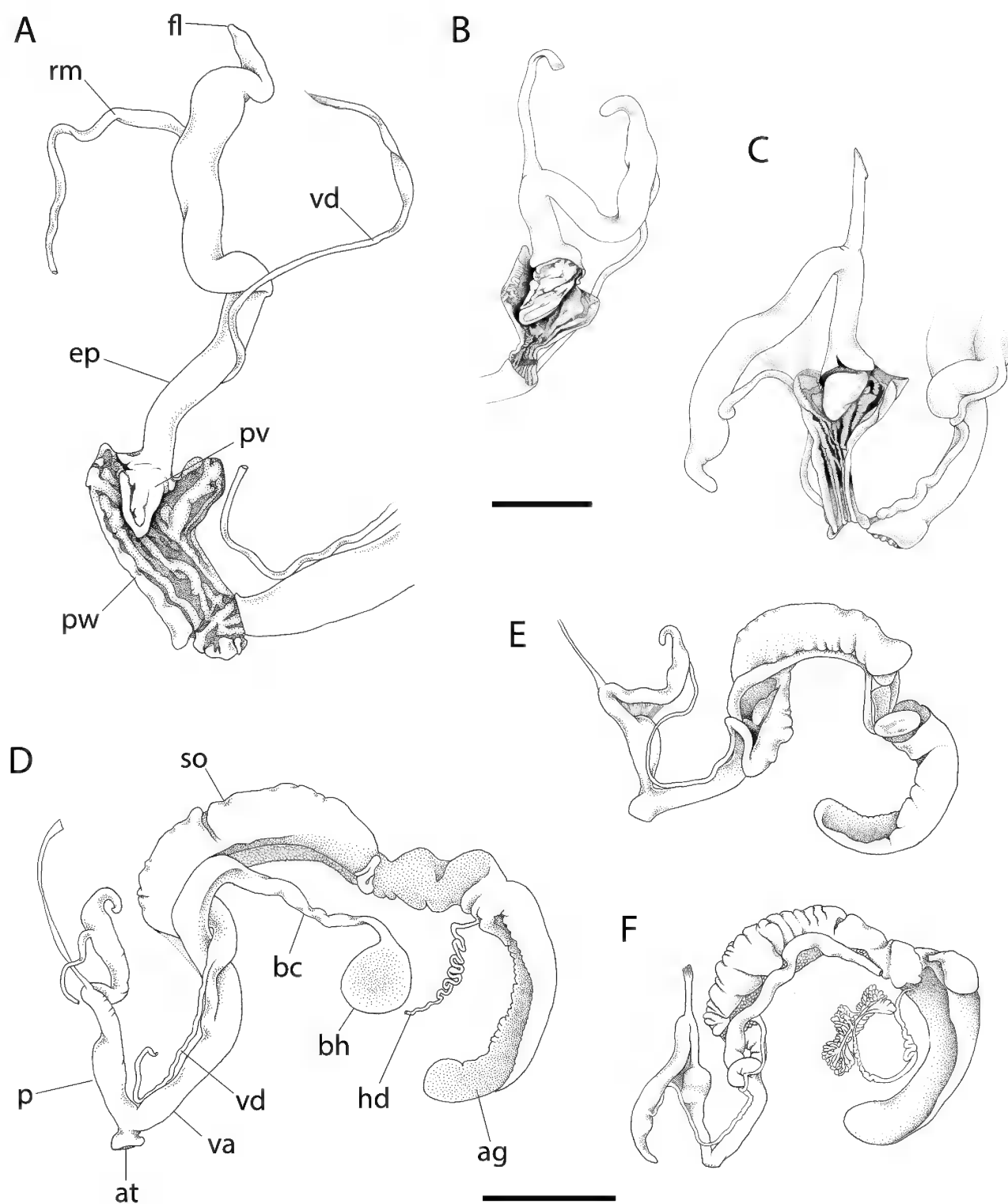


**Figure 6.** Scanning electron micrographs of shells of *Austrochloritis* (teleoconch viewed from above, protoconch viewed from above). (A, B) *Austrochloritis kaputarensis* AM C.478659, Mt Kaputar; (C, D) *Austrochloritis copelandensis* sp. nov., paratype, AM C.459997, Copeland Tops.

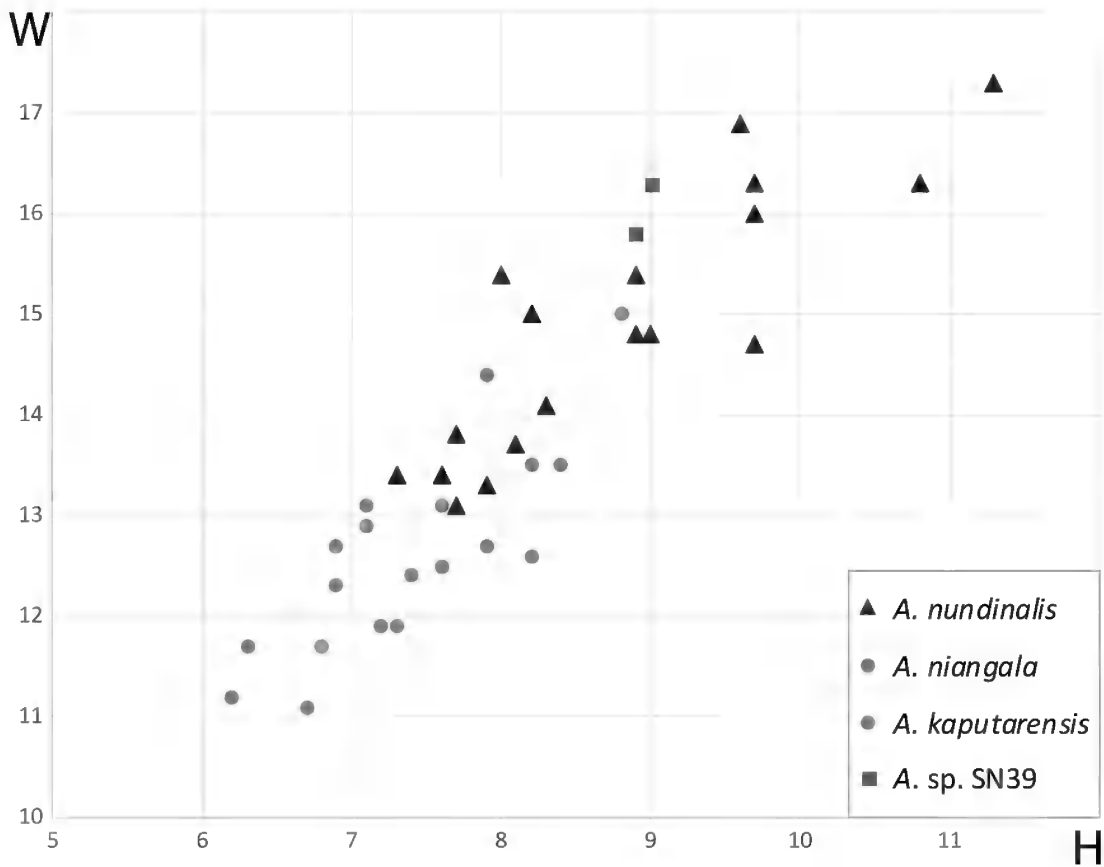
-31.25° 151.54°), AM C.575258 (3 d, Niangala-Weabonga road, -31.30° 151.37°), AM C.575450 (3 w, 1d, Niangala-Weabonga road, -31.30° 151.37°), AM C.557123 (2 d, 30 km N of Armidale, Thunderbolts Cave, -30.33° 151.67°), AM C.557124 (2 d, same as AM C.557123), AM C.519090 (1 d, Mt Kaputar NP, Coryah Gap, -30.28° 150.13°), AM C.480187 (3 w, same as AM C.519090), AM C.519095 (1 d, Mt Kaputar NP, West Kaputar Rock lookout, -30.28° 150.15°), AM C.519099 (10 d, Mt Kaputar NP, Barraba Track, -30.29° 150.18°), AM C.480188 (4 w, same as AM C.519099), AM C.478644 (4 d, Mt Kaputar NP, Barraba Track, -30.31° 150.21°), AM C.478832 (4 d, same as AM C.478644), AM C.478653 (5 d, Mt Kaputar NP, South East Fire trail, -30.32° 150.23°), AM C.478658 (8 d, Mt Kaputar NP, eastern park entrance, -30.32° 150.23°), AM C.478674 (3 d, Mt Kaputar NP, below Dawson's Spring, -30.28° 150.16°), AM C.477015 (1 w, Mt Kaputar NP, Dawson's Spring, -30.28° 150.16°), AM C.480193 (1 w, Mt Kaputar NP, 4.4 km up from Green Camp, -30.28° 150.12°), AM C.164945 (4 w, NW of Armidale, W of Guyra, Georges Mountain, -30.23° 151.25°), AM C.339673 (1 d, same as AM C.164945), AM C.339674 (1 d, same as AM C.164945), AM C.375155 (1 w, 1 d, 21.4 km W of Armidale on Bundarra Rd, -30.49° 151.48°), AM C.210134 (4 d, N of Armidale, Tilbuster Ponds, -30.36° 151.68°), AM C.561050 (3 w, 10 d, Georges Mountain, Basin NR, -30.23° 151.25°).

### Nomenclatural and taxonomic remarks

Both species, *A. niangala* and *A. kaputarensis*, were described in the same publication based on shell characters only. Their original descriptions are indicative of their rather close similarity. The purported differences are mainly in the length and density of periostracal setae. However, the reproductive anatomy was previously not documented. We are unable to identify any consistent morphological or anatomical difference between these two taxa. Shells are virtually identical in shape and size and no significant and consistent difference in the density and length of periostracal was observed. 16S sequences assigned to both taxa, respectively, differed from each other by on average 4.3 % p-distance, which may well be in the range of intraspecific genetic variation given the comparatively large geographic distances between the sequenced populations (Fig. 5). Based on the lack of consistent morpho-anatomical differentiation in concert with the rather low amount of mitochondrial differentiation, we consider both taxa as synonyms. Preference is here given to the name *A. niangala* by First Reviewers Choice. The candidate species *Austrochloritis* sp. NE3, which has been identified during curatorial work in the collections of the AM, is also considered as conspecific with *A. niangala* for exhibiting a consistent morpho-anatomy and also because it falls within the sub-clade formed by sequences of *A. niangala* (Fig. 1).



**Figure 7.** Reproductive anatomy of *Austrochloritis niangala*. (A–C) Penial anatomy: A, AM C.575450, *A. niangala*, Niangala; B, AM C.480188, *A. kaputarensis*, Mt Kaputar; C, AM C.375155, *Austrochloritis* sp. NE3, Bundarra; scale bar = 2 mm. (D–F) Reproductive system: D, AM C.575450, *A. niangala*, Niangala; E, AM C.480188, *A. kaputarensis*, Mt Kaputar; F, AM C.375155, *Austrochloritis* sp. NE3, Bundarra; scale bar = 5 mm.



**Figure 8.** Comparison of shell dimensions of *Austrochloritis nundinalis*, *A. niangala*, *A. kaputarensis*, and *A. copelandensis* sp. nov. by ordination of shell height against width.

### Description

**Shell** (Figs 2C–F, 3C–F, 6A,B). Medium sized ( $W=11.1$ – $15.0$  mm,  $H=6.2$ – $8.8$  mm,  $N = 3.2$ – $3.9$ ; for  $n = 20$ ; Table 1), turbanate to depressedly globose, with rounded to slightly shouldered whorls that regularly increase in diameter, sutures rather deeply incised; protoconch sculpture of rugose radials with coarse pustules at apex and with periostracal setae extending well on protoconch; teleoconch sculpture of low growth lines and corrugations with periostracal sculpture of rather straight, moderately widely spaced and occasionally long setae, interstitial microsculpture of very fine wavy periostracal ridgelets and scales; end of last whorl descending strongly below whorl plane on reaching sexual maturity; aperture moderately tilted forward from axis of coiling, without thickened or reflected outer lip and without sulcus behind lip; umbilicus moderately open with U-shaped profile; shell colour pale yellowish brown.

**Reproductive anatomy** (Fig. 7). Penis cylindrical, narrowing toward genital opening, no penial sheath, penial sculpture of corrugated interlocking longitudinal filaments, distally giving rise to longitudinal rows of strap-like filaments, epiphallus twice as long as penis, with well-developed finger—like epiphallic flagellum at distal end, penial verge broadly conical, with wide longitudinal groove, length equivalent to between about half and one third of length of penis, free; penial retractor attached to proximal third of epiphallus, vas deferens entering head of epiphallus through single pore just below base of epiphallic

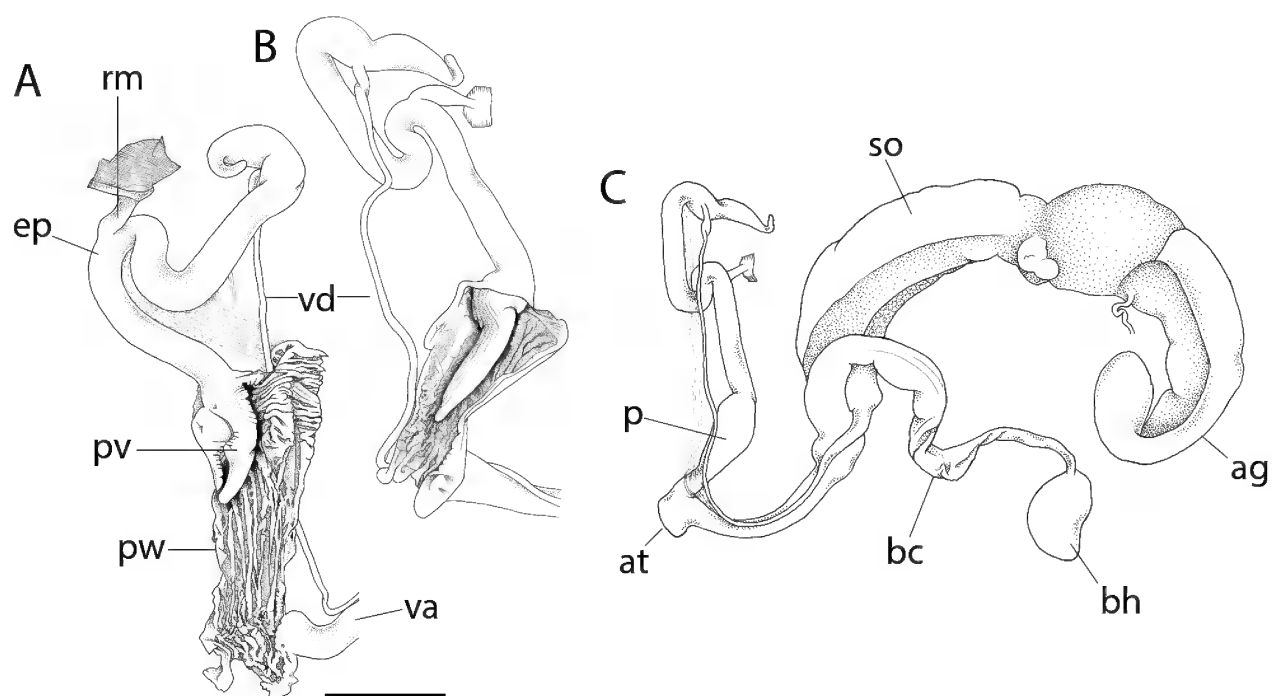
flagellum; vas deferens narrow to broad at its junction with apex of epiphallus, later tapering to a narrow tubule; vagina cylindrical, as long as penis, inner wall with prominent longitudinal anastomosing pilasters and filaments; bursa copulatrix long and broad, particularly at its base, folded or kinked several times and about as long as oviduct, with inflated bulb-like head, aligning with base of albumen gland; hermaphroditic duct inserting into head of talon.

### Comparative remarks

*Austrochloritis niangala* can be distinguished from *A. nundinalis* by its smaller shell (Fig. 8) and by having straight instead of curved periostracal setae. Both species exhibit a very similar reproductive anatomy, but differ somewhat in the relative length of the bursa copulatrix (longer in *A. nundinalis*) and the penial verge (occasionally partly attached to penial wall in *A. nundinalis*, free in *A. niangala*). Like *A. nundinalis*, the lack of a reflected outer lip and sulcus and the setae extending well onto the protoconch are shell features that distinguish *A. niangala* from most other congeners. Despite occurring in relative close proximity near Nundle, both species are separated by genetic p-distances of on average 7% (minimum 5.9 %).

Material from the Mt Kaputar NP previously described as *Australochloritis kaputarensis* does not consistently or significantly differ in shell or reproductive characters from material from near the type locality of *A. niangala* and is therefore considered as conspecific.





**Figure 9.** Reproductive anatomy of *Austrochloritis copelandensis* sp. nov. (A) Penial anatomy, paratype, AM C.575460, Copeland Tops; (B) penial anatomy, holotype, AM C.582897, Copeland Tops; (C) reproductive system, paratype, AM C.575460, Copeland Tops; scale bar = 3 mm.

### Distribution and ecology

*Austrochloritis niangala* lives in dry to moist sclerophyll forests on the New England Plateau from Mt Kaputar in the west to near Guyra in east and E of Tamworth in the south (Fig. 5). Most of its range is heavily fragmented into very small remnant patches of forests as large parts of the species' natural range has been cleared for agriculture.

### *Austrochloritis copelandensis* sp. nov.

urn:lsid:zoobank.org:act:8177FD12-CE11-4B65-92CD-F37658F02393

Figs 2G, 6C,D, 9A,B

**Holotype** AM C.582897 (1 w, dissected, sequenced; Fig. 2G) from NSW, Copeland Tops SCA, off Scone road, Hidden Treasure Walking Track, -32.00° 151.83°; leg. Köhler, Xie, Shea, 3/6/2018. **Paratypes** AM C.575460 (2 w, one dissected, sequenced), as for the holotype; AM C.459997 (1w, Copeland Tops SCA, Hidden Treasure Walking Track).

**Non-type material examined.** AM C.575265 (1 w, Bucketts Mountains off Bucketts Road nr Gloucester, Bucketts Scenic Walk, -32.00° 151.94°).

### Description

**Shell** (Figs 2G, 6C–D). Medium sized to large (W = 13–17 mm, H = 8.5–11 mm; for n = 4); discoidal in shape with a flat to low domed spire, with on average 4.5 rounded to slightly shouldered whorls that increase gradually in diameter; sutures deeply incised; protoconch sculpture of low radials with rugose pustules at apex and with periostracal setae extending well onto protoconch; teleoconch sculpture of low growth lines and corrugations

with periostracal sculpture of strongly curved, crowded and short setae; interstitial microsculpture of very fine wavy periostracal ridgelets and scales; end of last whorl descending strongly below whorl plane on reaching sexual maturity; aperture moderately tilted forward from axis of coiling, with thickened and strongly reflected white outer lip and with shallow sulcus behind lip; umbilicus widely open with U-shaped profile; shell colour from pale yellowish brown to reddish brown, sometimes with a darker mid peripheral colour band.

**Reproductive anatomy** (Fig. 9). Penis cylindrical, narrowing toward genital opening, no penial sheath; penial sculpture of corrugated interlocking transverse to longitudinal filaments, distally giving rise to longitudinal rows of strap-like filaments; epiphallus more than twice as long as penis, with well-developed finger-like epiphallallic flagellum at distal end, moderately long, broad at base, tapering to blunt apex and kinked; penial verge elongately conical and curved with tapering apex, free to partially attached to penial wall, vergic slit longitudinal along length of verge. Verge length equivalent to between about half to two thirds of length of penis. Penial retractor half the length of epiphallus from its base; vas deferens entering head of epiphallus through single pore just below base of epiphallallic flagellum; vas deferens narrow to broad at its junction with base of apex of epiphallus but later tapering to a narrow tubule; vagina cylindrical, as long as or one and one quarter longer than penis, inner wall with prominent longitudinal anastomosing pilasters and filaments; bursa copulatrix long and broad, particularly at its base, folded or kinked several times and as long as or slightly longer than oviduct with inflated bulb-like head, aligning with base of albumen gland; hermaphroditic duct inserting into head of talon.

## Comparative remarks

*Austrochloritis copelandensis* is conchologically rather similar to *A. mundinalis*, especially in regard to its comparatively large size (both still being smaller than *A. porteri*) (Fig. 8). However, both species differ from each other in that shells of similar size have about 0.5 more whorls in *A. copelandensis* than *A. mundinalis*. Shells of *A. copelandensis* differ from both *A. mundinalis* and *A. niangala* by having a well-reflected apertural lip and sulcus and a somewhat wider umbilicus. The reproductive anatomy of all three species is rather similar, but *A. copelandensis* differs from *A. mundinalis* and *A. niangala* by having a much longer and more slender penial verge. *Austrochloritis copelandensis* co-occurs with other *Austrochloritis* species: At the type locality, Copeland Tops, the other species resembles *A. nambucca* Iredale, 1943 while at the second known site, Bucketts Range, the second species is *A. disjuncta* (Gude, 1906). Both species are not closely related with *A. copelandensis* based on the mitochondrial phylogeny presented by Köhler *et al.* (2019).

## Distribution and ecology

This species lives in scree, dry vine thickets and dry rainforest in the, Manning Valley (Fig. 5), where it has been found under logs and in rock piles. Only two occurrences are currently known; both located in a distance of about 25 km from each other at altitudes of 236 and 348 m on sedimentary laminated siltstones and sandstones (Copeland Tops) or rhyolite (Bucketts Range) bedrock, respectively.

**ACKNOWLEDGEMENTS.** This study has been funded by the Australian Government through an ABRS Bush Blitz Grant to FK (TTC216-16), which is gratefully acknowledged. Special thanks are due to Bruce Jenkins, Sydney, who donated additional funds to support this project. Thanks are also due to Sue Lindsay, Macquarie University, and Anders Hallan (AM) for producing SEM micrographs. We appreciate the comments of two reviewers, which helped to improve the clarity of this manuscript.

## References

- Ballard, J. W. O., and M. C. Whitlock. 2004. The incomplete natural history of mitochondria. *Molecular Ecology* 13(4): 729–744.  
<https://doi.org/10.1046/j.1365-294X.2003.02063.x>
- Castresana, J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17(4): 540–552.  
<https://doi.org/10.1093/oxfordjournals.molbev.a026334>
- Chiba, S. 1999. Accelerated evolution of land snails *Mandarina* in the oceanic Bonin Islands: Evidence from mitochondrial DNA sequences. *Evolution* 53(2): 460–471.  
<https://doi.org/10.1111/j.1558-5646.1999.tb03781.x>
- Criscione, F., and F. Köhler. 2013. Conserved shell disguises diversity in *Mesodontrachia* land snails from the Australian Monsoon Tropics (Gastropoda: Camaenidae). *Zoologica Scripta* 42(4): 389–405.  
<https://doi.org/10.1111/zsc.12011>
- Criscione, F., and F. Köhler. 2014a. Molecular phylogenetics and comparative anatomy of Kimberleytrachia Köhler, 2011—a genus of land snail endemic to the coastal Kimberley, Western Australia with description of new taxa (Gastropoda, Camaenidae). *Contributions to Zoology* 83(4): 245–267.  
<https://doi.org/10.1163/18759866-08304003>
- Criscione, F., and F. Köhler. 2014b. Molecular phylogeny and taxonomic revision of the genera *Baudinella* Thiele, 1931, *Retroterra* Solem, 1985 and *Molema* Köhler, 2011 endemic to the coastal Kimberley, Western Australia (Gastropoda, Camaenidae). *Journal of Zoological Systematics and Evolutionary Research* 52(4): 273–284.  
<https://doi.org/10.1111/jzs.12065>
- Criscione, F., and F. Köhler. 2016a. Snails in the desert: Assessing the mitochondrial and morphological diversity and the influence of aestivation behavior on lineage differentiation in the Australian endemic *Granulomelon* Iredale, 1933 (Stylommatophora: Camaenidae). *Molecular Phylogenetics and Evolution* 94: 101–112.  
<https://doi.org/10.1016/j.ympev.2015.08.021>
- Criscione, F., and F. Köhler. 2016b. Phylogenetic systematics of the land snail *Basedowena* from the Australian arid zone: taxonomic revision with description of new taxa (Stylommatophora: Camaenidae). *Invertebrate Systematics* 30(4): 370–386.  
<https://doi.org/10.1071/IS16006>
- Davison, A., and B. Clarke. 2000. History or current selection? A molecular analysis of ‘area effects’ in the land snail *Cepaea nemoralis*. *Proceedings of the Royal Society B: Biological Sciences* 267: 1399–1405.  
<https://doi.org/10.1098/rspb.2000.1156>
- Folmer, O., M. Black, W. Hoeh, R. Lutz, and R. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.
- Funk, D. J., and K. E. Omland. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology and Systematics* 34: 397–423.  
<https://doi.org/10.1146/annurev.ecolsys.34.011802.132421>
- Iredale, T. 1943. Guide to the land shells of New South Wales. Part V. *Australian Naturalist* 11: 61–69.
- Johnson, M. S., S. Stankowski, P. G. Kendrick, Z. R. Hamilton, and R. J. Teale. 2016. Diversity, complementary distributions and taxonomy of *Rhagada* land snails (Gastropoda: Camaenidae) on the Burrup Peninsula, Western Australia. *Invertebrate Systematics* 30(4): 323–334.  
<https://doi.org/10.1071/IS15046>
- Kalyaanamoorthy, S., B. Q. Minh, T. K. F. Wong, A. von Haeseler, and L. S. Jermin. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14(6): 587–589.  
<https://doi.org/10.1038/nmeth.4285>
- Katoh, K., K. Misawa, K. Kuma, and T. Miyata. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30(14): 3059–3066.  
<https://doi.org/10.1093/nar/gkf436>
- Köhler, F. 2011. The camaenid species of the Kimberley Islands, Western Australia (Stylommatophora: Helicoidea). *Malacologia* 54(1–2): 203–406.  
<https://doi.org/10.4002/040.054.0108>
- Köhler, F. 2016. Rampant taxonomic incongruence in a mitochondrial phylogeny of *Semisulcospira* freshwater snails from Japan (Cerithioidea: Semisulcospiridae). *Journal of Molluscan Studies* 82(2): 268–281.  
<https://doi.org/10.1093/mollus/eyv057>
- Köhler, F. 2017. Against the odds of unusual mtDNA inheritance, introgressive hybridisation and phenotypic plasticity: systematic revision of Korean freshwater gastropods (Semisulcospiridae, Cerithioidea). *Invertebrate Systematics* 31(3): 249–268.  
<https://doi.org/10.1071/IS16077>
- Köhler, F., and I. Burghardt. 2016. Cryptic diversity in a widespread land snail: revision of the genus *Xanthomelon* Martens, 1860 from the Australian Monsoon Tropics (Pulmonata, Camaenidae). *Zoologica Scripta* 45(2): 127–144.  
<https://doi.org/10.1111/zsc.12144>

- Köhler, F., F. Criscione, and M. Shea. 2020 in press. A mitochondrial phylogeny uncovers taxonomic ambiguity and complex phylogeographic patterns in the eastern Australian land snail *Austrochloritis* (Stylommatophora, Camaenidae). *Journal of Zoological Systematics and Evolutionary Research* 2020 e1–e16.  
<https://doi.org/10.1111/jzs.12366>
- Köhler, F., and G. Deen. 2010. Hybridisation as potential source of incongruence in the morphological and mitochondrial diversity of a Thai freshwater gastropod (Pachychilidae, *Brotia* H. Adams, 1866). *Zoosystematics and Evolution* 86(2): 301–314.  
<https://doi.org/10.1002/zoos.201000013>
- Minh, B. Q., M. A. Nguyen, and A. von Haeseler. 2013. Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* 30(5): 1188–1195.  
<https://doi.org/10.1093/molbev/mst024>
- Nguyen, L.-T., H. A. Schmidt, A. von Haeseler, and B. Q. Minh. 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating Maximum-Likelihood phylogenies. *Molecular Biology and Evolution* 32(1): 268–274.  
<https://doi.org/10.1093/molbev/msu300>
- O'Neill, C., M. S. Johnson, Z. R. Hamilton, and R. J. Teale. 2014. “Molecular phylogenetics of the land snail genus *Quistrachia* (Gastropoda: Camaenidae) in northern Western Australia.” *Invertebrate Systematics* 28(3): 244–257.  
<https://doi.org/10.1071/IS13045>
- Shea, M., and F. Köhler. 2019. Towards a systematic revision of the eastern Australian land snail *Austrochloritis* Pilsbry, 1891 (Eupulmonata, Camaenidae): Re-description of its type species, *A. porteri* (Cox, 1866). *Records of the Australian Museum* 71(4): 111–120.  
<https://doi.org/10.3853/j.2201-4349.71.2019.1699>
- Sites, J. W., and J. C. Marshall. 2004. Operational criteria for delimiting species. *Annual Review of Ecology Evolution and Systematics* 35: 199–227.  
<https://doi.org/10.1146/annurev.ecolsys.35.112202.130128>
- Stanisic, J., M. Shea, D. Potter, and O. Griffiths. 2010. *Australian land snails. 1. A field guide to eastern Australian species*. Riviere des Anguilles, Mauritius: Bioculture Press.
- Sutcharit, C., T. Asami, and S. Panha. 2007. Evolution of whole-body enantiomorphy in the tree snail genus *Amphidromus*. *Journal of Evolutionary Biology* 20(2): 661–672.  
<https://doi.org/10.1111/j.1420-9101.2006.01246.x>
- Taylor, J. P. A., M. S. Johnson, and S. Stankowski. 2015. Molecular phylogenetics and complementary geographical distributions of species of the Western Australian land snail genera *Plectorhagada* Iredale, 1933 and *Strepsitaurus* Solem, 1997 (Gastropoda: Camaenidae). *Zoological Journal of the Linnean Society* 174(2): 305–321.  
<https://doi.org/10.1111/zoj.12238>
- Whelan, N. V., and E. E. Strong. 2016. Morphology, molecules and taxonomy: extreme incongruence in pleurocerids (Gastropoda, Cerithioidea, Pleuroceridae). *Zoologica Scripta* 45(1): 62–87.  
<https://doi.org/10.1111/zsc.12139>

# Neotype Designation for the Australian Pig-footed Bandicoot *Chaeropus ecaudatus* Ogilby, 1838

KENNY J. TRAVOUILLO<sup>1</sup> , HARRY PARNABY<sup>2</sup>  AND SANDY INGLEBY<sup>2</sup> 

<sup>1</sup> Western Australian Museum,  
Locked Bag 49, Welshpool DC WA 6986, Australia

<sup>2</sup> Australian Museum Research Institute,  
Australian Museum, 1 William Street, Sydney NSW 2010, Australia

**ABSTRACT.** The original description of the now extinct Australian Pig-footed Bandicoot *Chaeropus ecaudatus* Ogilby, 1838 was based on one specimen from which the tail was missing. Re-examination of the skull thought to be the holotype of *C. ecaudatus*, revealed that it was associated with a skeleton with caudal vertebrae, thereby negating its type status. The holotype has not been reliably sighted since 1860 and is presumed lost as it has not been identified in world collections. We designate PA422, a skull and partial skeleton in the Australian Museum, Sydney as neotype for *Chaeropus ecaudatus*. This arose from a recent taxonomic revision of *Chaeropus* that recognized two subspecies of *C. ecaudatus*, prompting resolution of the type material of nominate *ecaudatus*.

## Introduction

The extinct Pig-footed Bandicoot *Chaeropus ecaudatus* Ogilby, 1838 has long been regarded as a monotypic species within a monotypic genus following the decision of Iredale & Troughton (1934). Jackson & Groves (2015) give a summary of the taxonomic history of the genus. In their generic revision, Travouillon *et al.* (2019) described a new species and recognized two subspecies within *C. ecaudatus*. Their taxonomic work required resolution of type material for nominate *C. ecaudatus*, the holotype of which was thought to be lost (Parnaby *et al.*, 2017). Although Travouillon *et al.* (2019) concluded that the holotype was PA422 in the Australian Museum (AM), this has subsequently been invalidated, necessitating designation of a neotype for *C. ecaudatus ecaudatus*.

The original description of *Chaeropus ecaudatus* was based on the drawings and field notes of Sir Thomas Mitchell who collected a single specimen near the Murray River in New South Wales. The specimen did not have a tail, which

led Ogilby (1838), who never examined the specimen then in the Australian Museum, Sydney, to name the species “*ecaudatus*” meaning tailless. Mahoney & Ride (1985) concluded that Mitchell’s original specimen was listed in the first AM catalogue (Bennett, 1837: 7) as number 35, a female, which is listed without a name as “A new and undescribed marsupial animal, of singular form”. Their conclusion appears to be based on elimination of other unnamed new mammal species listed by Bennett, which Mahoney (1982) had established to be rodent taxa. Krefft (1864) lists only two specimens of *Chaeropus ecaudatus* in the Australian Museum collection, an adult male from “Gall Creek”, which originally came from Museum Victoria (MV), and a skull from the lower Murray, which he thought was Sir Thomas Mitchell’s original specimen. Gerard Krefft was first employed at the AM in 1860. Krefft (1870) states that he found the original skull “10 years ago” but did not locate the associated skin, which he concluded had been destroyed through the neglect of his curatorial predecessors. Troughton (1932) believed the holotype disappeared from

**Keywords:** Peramelemorphia; holotype; *Chaeropus*; neotype; museum specimen; Gerard Krefft; Sir Thomas Mitchell


**Zoobank registration:** urn:lsid:zoobank.org:pub:0C2213A9-4CF9-45A4-A5D5-18B489FD4C9E

**Corresponding author:** Kenny J. Travouillon [Kenny.Travouillon@museum.wa.gov.au](mailto:Kenny.Travouillon@museum.wa.gov.au)

**Received:** 26 August 2019 **Accepted:** 3 June 2020 **Published:** 29 July 2020 (in print and online simultaneously)

**Publisher:** The Australian Museum, Sydney, Australia (a statutory authority of, and principally funded by, the NSW State Government)

**Citation:** Travouillon, Kenny J., Harry Parnaby and Sandy Ingleby. 2020. Neotype designation for the Australian Pig-footed Bandicoot *Chaeropus ecaudatus* Ogilby, 1838. *Records of the Australian Museum* 72(3): 77–80. <https://doi.org/10.3853/j.2201-4349.72.2020.1761>

**Copyright:** © 2020 Travouillon, Parnaby, Ingleby. This is an open access article licensed under  Creative Commons Attribution 4.0 International License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original authors and source are credited.



the collection soon after it was named and Mahoney & Ride (1988) and Parnaby *et al.* (2017) concluded that the holotype could not be identified amongst the specimens now in the AM. There appear to be no illustrations or measurements of the holotype skull which represents a major impediment to its rediscovery. Travouillon *et al.* (2019) suggested that AM PA421 seemed to match Krefft's (1864) specimen from "Gall Creek" and that AM PA422 was the holotype from the lower Murray River collected by Mitchell. Their conclusions were based on the assumption that the number of 19th century specimens of *C. ecaudatus* in the AM collection had been reliably determined, which has subsequently been found to be incorrect. After re-examining AM PA422, we noticed a number of inconsistencies that negate its type status. First, the specimen that was thought to be a single skull was instead associated with a partial skeleton that included 13 caudal vertebrae. The presence of a tail means that this specimen cannot be the holotype of *Chaeropus ecaudatus*. Additionally, the sex of the specimen, male, recorded on the label, did not match the sex recorded by Mitchell (i.e. a female). The locality is noted as "Murray River" as for the holotype, but no collector is recorded. Since AM PA422 is not the holotype of *C. ecaudatus*, and no trace of the holotype can be found, we propose here to designate a neotype. Given that Travouillon *et al.* (2019) treated AM PA422 as the holotype in their revision of the genus, we consider it appropriate to designate AM PA422 as the neotype.

## Systematics

Order Peramelemorphia Kirsch, 1968

(Aplin & Archer, 1987)

Superfamily Perameloidea Gray, 1825

Family Chaeropodidae Gill, 1872 (Groves, 2005)

Genus *Chaeropus* Ogilby, 1838

## *Chaeropus ecaudatus* Ogilby, 1838

### *Chaeropus ecaudatus ecaudatus*

Ogilby, 1838

Fig. 1

**Neotype.** Australian Museum PA422, juvenile male skull and the associated partial skeleton (Fig. 1), collector and date of collection unknown.

**Type locality.** The only locality information entered by Secretary Palmer in the PA catalogue is "Murray River".

**Remarks.** The skull is clearly that of a juvenile, with deciduous premolars still being in place and incompletely erupted upper 4th molars. The skeleton also shows evidence of being that of a juvenile, with incomplete fusion of the epiphyses of the long bones of the limbs. This is most obvious in the humerus. The skeleton has 4 cervical vertebrae represented including the axis (C2) and C3 to C5. The atlas (C1) and C6 are missing. A total of 10 thoracic vertebrae are present, though it is difficult to be certain which one is

missing as only the last 4 are still articulated. All 6 lumbar vertebrae are present, as well as the first sacral vertebra. Some of the caudal vertebrae are preserved with 6 chevrons and includes Ca01–Ca13, though only the anterior half of Ca13 is present. The right scapula, humerus and ulna are present, but only the left ulna is present. Two thoracic bones are present. The fused left and right tibia and fibula are present, as well as all bones of the left and right pes.

Australian Museum PA422 was selected as the neotype because it is the only sexed specimen displaying key diagnostic dental criteria, some of which are only seen in unworn teeth. Only two specimens are complete enough to be considered for neotype selection, AM PA422 and NMV C2900. The latter is an unsexed adult with teeth that are too worn to reveal key diagnostic characters. As a result, the juvenile dentition of the sexed AM PA422 is taxonomically more informative as a neotype than NMV C2900. AM PA422 has been fully described in Travouillon *et al.* (2019) and was the principal comparative specimen used in the species diagnosis of *Chaeropus yirratji* Travouillon *et al.* (2019).

## Discussion

The collecting locality of Mitchell's original specimen has been determined by Wakefield (1966), who mapped the approximate locality in his fig. 1. His figure indicates that the locality is c. 10 miles (16 km) SE of the junction of the Murray and Murrumbidgee Rivers, Victoria. Article 76.3 of the Code (ICZN, 1999) states that the collecting locality of the neotype becomes the new type locality, irrespective of previously published statement of the type locality. A total of 12 modern specimens of *C. ecaudatus ecaudatus* are known in world collections (as well as 7 fossil specimens), some of which have precise locality data. However, PA422 is one of the two (the other being NMV C2900) that consists of a skull and post-cranial skeleton. Displacing the original type locality with the vague "Murray River" associated with the neotype is a regressive step but appears to be required by the current version of the Code. We would prefer to restrict the type locality of the neotype to that of the original type locality and hope that the next edition of the Code can accommodate situations such as this.

It is very unlikely that PA422 is the original specimen collected by Mitchell. The partial skeleton associated with skull PA422 cannot be his original specimen because it contains caudal vertebrae yet the tail was reportedly absent from Mitchell's specimen. Further, it consists of a complete set of skeletal elements of manus and pes that would have invariably been included in the preparation of a skin mount. The skull and post-cranial bones are both of a juvenile animal. The occipital region of the skull is missing. This prevents absolute confirmation that the skull has been correctly matched with the partial skeleton, but as both are of a juvenile individual, we accept that they are unlikely to have been mismatched at an earlier time.

As far as we are aware, the remarks by Krefft (1870) are the last record of the holotype of *C. ecaudatus*. Ogilby (1892) states that the holotype is in the AM collection but it is not clear if this was conjecture or if he actually sighted the specimen. Iredale and Troughton (1932: v) were critical of Ogilby (1892), which they imply was largely a "desk top" study with little reference to specimens in the collection. We have not found any further reference to the type specimen





**Figure 1.** Australian Museum PA422, neotype skull and partial skeleton of *Chaeropus ecaudatus* Ogilby 1838. Scale = 5 cm.

in the literature or archival documents. Troughton (1930: 179) remarked that “This type specimen was lodged in the Australian Museum, but some time afterwards unfortunately disappeared.” His statement is significant because he was well placed to draw on the “Institutional memory” of the AM from zoologists who worked or were associated with the AM throughout the decades immediately after the end of Krefft’s curatorship. For example, Troughton joined the AM in 1908 and was a contemporary of E. P. Ramsay, who was a research associate at the AM until 1915 and Krefft’s immediate curatorial successor. Troughton was also a contemporary of R. Etheridge Jr, who had replaced Ramsay as Director in 1895.

We have found only two specimens of *C. ecaudatus* in the early specimen registers of the AM. Both were registered by Secretary Palmer in the “Palmer” register at an unrecorded date but probably 1877 or 1878. Both are listed as “*Chaeropus castanotus*” (a misspelling of *Chaeropus castanotis*, a junior synonym of *Chaeropus ecaudatus*) and “Murray River”. Palmer listed PA421 as a “Mounted skin” and PA422 as a “skeleton” but Palmer did not enter any further information, perhaps because nothing further was associated with the specimen labels. A subsequent entry in the Palmer register indicates that both specimens were received from the “Melbourne Museum”. This entry was probably made during a specimen inventory around 1907

(see Parnaby *et al.*, 2017: 288) but remains problematic. Several specimens were received from Museum Victoria during the 1860s and possibly the early 1870s but the poor documentation of all of the early mammal specimens in the AM at that time prevents a reliable determination of the provenance of surviving specimens. The exact number received from the MV also remains unclear, some of which could have been sent to other institutions in the ensuing century. The total number of specimens of *C. ecaudatus* held by the AM during the 19th century thus remains unknown and not all specimens were necessarily registered at that time. Further, it is not known how many specimens of *C. ecaudatus* had been obtained by Krefft at the time his association with the AM was terminated in 1874. Krefft (1870) states “The animal is still rare, and after endless correspondence I obtained one; two more have since been captured by my friend, Mr John Williams of Gall Gall, who is only waiting an opportunity to send them to Sydney.” Williams was a local resident who assisted the Blandowski Expedition of 1856–1857. It is not known if Krefft ever received the specimens. It has not yet been established how many specimens of *C. ecaudatus* existed in the AM collection by the end of Krefft’s curatorship in 1874. The AM collection could have contained perhaps five specimens in addition to the holotype skull: perhaps two specimens from MV, and possibly up to three other specimens mentioned by Krefft

(1870). Inadequate documentation of material exchanged out of the AM collection during the 19th century is a further consideration.

Perhaps the skull of Mitchell's original specimen disappeared around the time of Krefft's dismissal from the AM in 1874, but we are not implying that Krefft was necessarily responsible for its fate. Several key specimens in the AM collection have not been sighted since his dismissal (see Parnaby *et al.*, 2017: 289).

**ACKNOWLEDGEMENTS.** We thank the Australian Biological Resources Study (ABRS) for providing the funding that helped undertake this taxonomic project. We thank Dr Vanessa Finney and Patricia Egan (AM Archives, Rare Books and Library Collections) who helped us locate documents in their care.

## References

- Aplin, K. P., and M. Archer. 1987. Recent advances in marsupial systematics with a new syncretic classification. In *Possums and Opossums, Studies in Evolution*, ed. M. Archer, pp. xv–lxi. Sydney, Australia: Surrey Beatty and Sons.
- Bennett, G. 1837. *Catalogue of the Specimens of Natural History and Miscellaneous Curiosities Deposited in the Australian Museum*. [Australian Museum Catalogue No. 1]. Sydney: James Tegg and Co. 71 pp.
- Gill, T. 1872. Arrangement of the families of mammals with analytical tables. *Smithsonian Miscellaneous Collections* 11: 1–98.  
<https://doi.org/10.5962/bhl.title.14607>
- Gray, J. E. 1825. An outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. *Annals of Philosophy* 10(2): 337–344.
- Groves, C. 2005. Order Peramelemorphia. In *Mammal Species of the World: A Taxonomic and Geographic Reference (3rd ed)*, ed. D. E. Wilson and D. M. Reader, pp. 38–42. Baltimore, USA: The Johns Hopkins University Press.
- ICZN (International Commission for Zoological Nomenclature). 1999. *International Code of Zoological Nomenclature. Fourth edition*. London: The International Trust for Zoological Nomenclature. xxix + 306 pp.
- Iredale, T., and E. L. G. Troughton. 1934. A check-list of the mammals recorded from Australia. *Australian Museum Memoir* 6: 1–122.  
<https://doi.org/10.3853/j.0067-1967.6.1934.516>
- Jackson, S. M., and C. P. Groves. 2015. *Taxonomy of Australian Mammals*. Melbourne, Victoria: CSIRO Publishing. 529 pp.  
<https://doi.org/10.1071/9781486300136>
- Kirsch, J. A. W. 1968. Prodrum of the comparative serology of Marsupialia. *Nature* 217: 418–420.  
<https://doi.org/10.1038/217418a0>
- Krefft, G. 1864. *Catalogue of Mammalia in the collection of the Australian Museum. Australian Museum Catalogue No. 2*. Sydney: Trustees of the Australian Museum. 2 + 134 + 2 pp.
- Krefft, G. 1870. Letter to the Editor (re *Chaeropus ecaudatus*). *Australian Town and Country Journal* II(42): 17, col. 1, 22 October.
- Mahoney, J. A. 1982. Identities of the rodents (Muridae) listed in T. L. Mitchell's *Three expeditions into the interior of eastern Australia, with descriptions of the recently explored region of Australia Felix, and of the present colony of New South Wales* (1st ed., 1838; 2nd ed., 1839). *Australian Mammalogy* 5(1&2): 15–36.
- Mahoney, J. A., and W. D. L. Ride. 1988. Peramelidae. In *Zoological Catalogue of Australia Vol. 5. Mammalia*, ed. D. W. Walton, pp. 36–42. Canberra: Australian Government Publishing Service.
- Ogilby, J. D. 1892. *Catalogue of Australian Mammals, with Introductory Notes on General Mammalogy*. Sydney: Trustees, Australian Museum. xvi + 142 pp.  
<https://doi.org/10.5962/bhl.title.1130>
- Ogilby, W. 1838. On a new species of marsupial animal by Major Mitchell on the banks of the Murray River in New South Wales. *Proceedings of the Zoological Society of London* 6: 25–27.
- Parnaby, H. E., S. Ingleby, and A. Divljan. 2017. Type specimens of non-fossil mammals in the Australian Museum, Sydney. *Records of the Australian Museum* 69(5): 277–420.  
<https://doi.org/10.3853/j.2201-4349.69.2017.1653>
- Troughton, E. L. G. 1932. Australian furred animals, their past, present and future. *Australian Zoologist* 7(3): 173–193.
- Travouillon, K. J., B. F. Simoes, R. Portela Miguez, S. Brace, P. Brewer, D. Stemmer, G. J. Price, J. Cramb, and J. Louys. 2019. Hidden in plain sight: reassessment of the pig-footed bandicoot, *Chaeropus ecaudatus* (Peramelemorphia, Chaeropodidae), with a description of a new species from central Australia, and use of the fossil record to trace its past distribution. *Zootaxa* 4566(1): 1–69.  
<https://doi.org/10.11646/zootaxa.4566.1.1>
- Wakefield, N. A. 1966. Mammals of the Blandowski Expedition to north-western Victoria, 1856–57. *Proceedings of the Royal Society of Victoria* 79: 371–391.

# Ceriantharia (Cnidaria) from Australia, New Zealand and Antarctica with Descriptions of Four New Species

SÉRGIO N. STAMPAR<sup>1</sup>, V. SADIE MILLS<sup>2</sup> AND STEPHEN J. KEABLE<sup>3</sup>

<sup>1</sup> Laboratório de Evolução e Diversidade Aquática—LEDA, Departamento de Ciências Biológicas,  
Universidade Estadual Paulista (UNESP), FCL/Assis, Av. Dom Antônio, 2100,  
19806-900, Assis, SP, Brazil

<sup>2</sup> NIWA Invertebrate Collection, National Institute of Water and Atmospheric Research,  
301 Evans Bay Parade Hataitai, 6021 Wellington, New Zealand

<sup>3</sup> Australian Museum Research Institute,  
Australian Museum, 1 William Street, Sydney NSW 2010, Australia

**ABSTRACT.** The fauna of Ceriantharia (tube-anemones) in the South Pacific is poorly studied with only four shallow-water species formally described and these animals are known from few regions in very specific reports. Cerianthids are organisms that live in a tube constructed with a special type of cnidae and are currently grouped in an exclusive subclass of Anthozoa. This study addresses specimens from three natural history collections, the Australian Museum and the Museum and Art Gallery of the Northern Territory (both Australia), and the National Institute of Water & Atmospheric Research (NIWA) Invertebrate Collection (New Zealand), focusing on specimens from the Coral Sea, Tasman Sea and Antarctic Ocean. As a result, four new species are described and one synonymized. This highlights the ongoing need for taxonomic studies in the region, especially for marine organisms. Also, in this study, we offer tables with morphological characters that can be useful for species identification in each genus.

## Introduction

Members of the subclass Ceriantharia are often the focus of photographic records in several regions of the world, but especially in areas where diving activities are concentrated (Stampar *et al.*, 2010, 2016a), including Australia and New Zealand (e.g., Grange & Brook, 2010; Wallace & Crowther, 2019). Despite this, Ceriantharia diversity is poorly studied in most parts of the world, especially because of the difficulties in sampling (Stampar *et al.*, 2016a). The Tasman Sea, between Australian and New Zealand coasts, is well studied for some taxa and locations (e.g., Polychaeta—Hutchings, 1992; Williams, 2019) but is contiguous with the Southern

Ocean, in which the level of biodiversity exploration is still incipient (Butler *et al.*, 2010; Griffiths, 2010). Within the Tasman Sea, there are only four species of Ceriantharia recorded and these are so far known from very limited localities. From Australia, *Pachycerianthus nobilis* Haddon & Shackleton, 1893, was described as a member of the genus *Cerianthus* from Torres Strait, Queensland. *Arachnanthus australiae* Carlgren (1937) is from Low Island (north of Port Douglas) also in Queensland. Two species were described by from Sydney Harbor, New South Wales, *Pachycerianthus delwyna* Carter, 1995 and *P. longistriatus* Carter, 1995. The state of knowledge about Ceriantharia from New Zealand is substantially poorest, because there are few records, without

**Keywords:** taxonomy; South Pacific; marine invertebrates; deep sea

**Zoobank registration:** urn:lsid:zoobank.org:pub:62E3C79A-499F-48DE-AFD9-111D52235D33

**Corresponding author:** Sérgio N. Stampar [sergio.stampar@unesp.br](mailto:sergio.stampar@unesp.br)

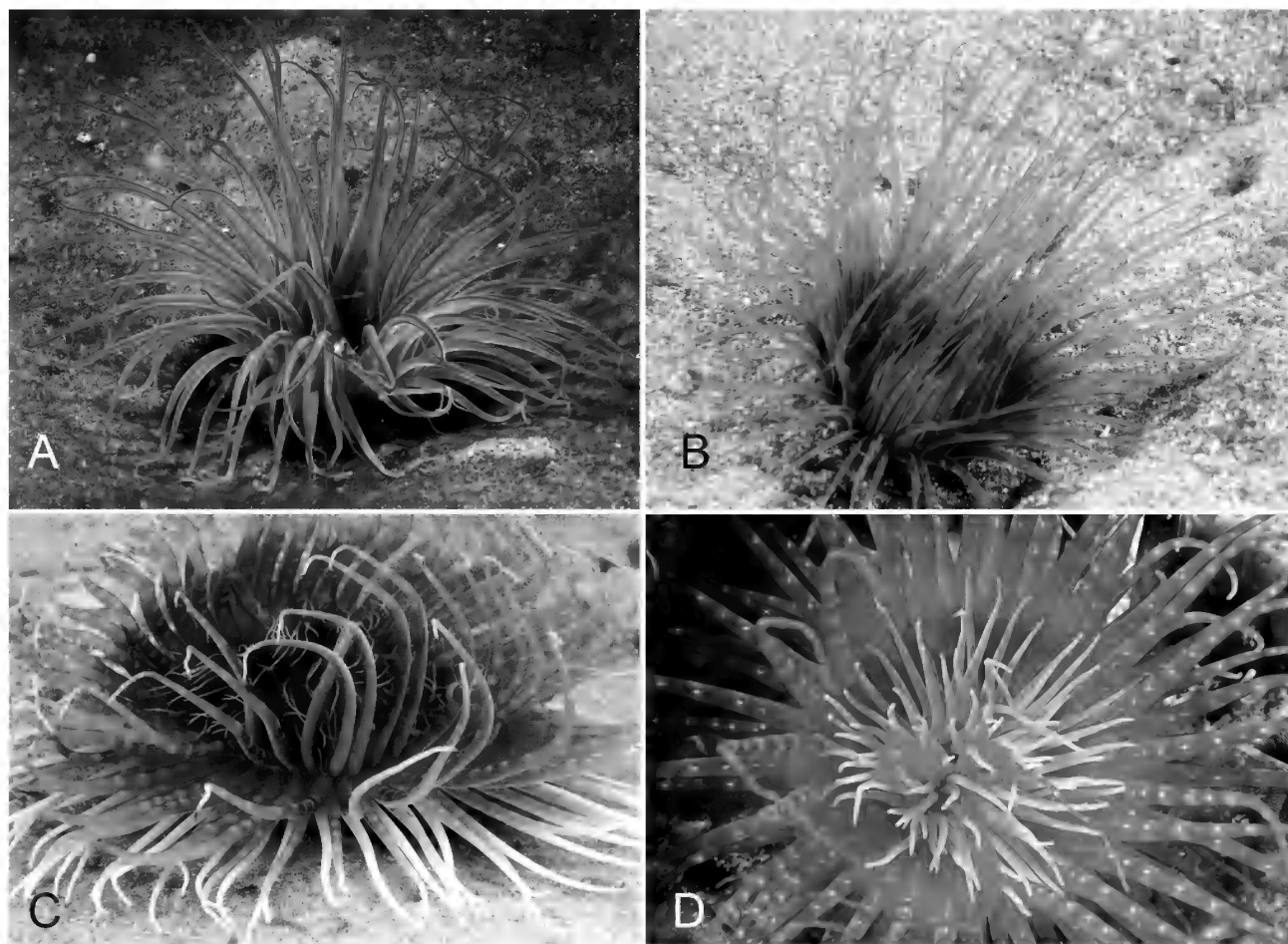
**Received:** 29 January 2020 **Accepted:** 8 June 2020 **Published:** 29 July 2020 (in print and online simultaneously)

**Publisher:** The Australian Museum, Sydney, Australia (a statutory authority of, and principally funded by, the NSW State Government)

**Citation:** Stampar, Sérgio N., V. Sadie Mills, and Stephen J. Keable. 2020. Ceriantharia (Cnidaria) from Australia, New Zealand and Antarctica with descriptions of four new species. *Records of the Australian Museum* 72(3): 81–100. <https://doi.org/10.3853/j.2201-4349.72.2020.1762>

**Copyright:** © 2020 Stampar, Mills, Keable. This is an open access article licensed under ■ Creative Commons Attribution 4.0 International License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original authors and source are credited.





**Figure 1.** Specimens of *Pachycerianthus delwynae* in New South Wales, Australia. (A, B) Tentacles with longitudinal lines and (C, D) banded tentacles. Images: Tony Strazzani.

any identification except “*Ceriantharia*”, “*Cerianthus*” or “*Pachycerianthus*”. Doak (1971) describes the discovery of a cerianthid on a night dive at the Poor Knights Islands in an open sandy section of a rocky wall. Grange *et al.* (1981) mention an undescribed species of cerianthid anemone, probably in genus *Cerianthus* observed dominating the soft sediment community in Long Sound, Fiordland. Cairns *et al.* (2009) discuss the existence of two undescribed species and also the occurrence of larvae of the genus *Arachnanthus*. Grange & Brook (2010) report the occurrence of two species of *Cerianthus* (*Cerianthus* sp.1 and *Cerianthus* sp.2) and one species of *Pachycerianthus* sp., however, there is limited discussion about how these identifications were made and availability of material for further examination.

This study addresses this knowledge gap, reviewing previous records and describes new species of two genera, *Ceriantheopsis* and *Pachycerianthus* from the South Pacific Ocean, including the Coral Sea, Tasman Sea and Antarctic Ocean. Additional information on characters used to differentiate species in these genera is also provided.

## Material and methods

Ceriantharia from the Australian Museum, Sydney (AM), Museum and Art Gallery of the Northern Territory, Australia (NTM) and National Institute of Water & Atmospheric Research (NIWA) Invertebrate Collection (NIC) (New Zealand) were studied, totalling 35 specimens. Anatomical study of the polyps and cnidome were based on criteria defined by several authors (van Beneden, 1897; Carlgren, 1912; den Hartog, 1977; Stampar *et al.*, 2014, 2016b). Specimens were sectioned through the ventral side (opposite to the siphonoglyph) using surgical scalpels (carbon steel), then the dissected polyp was fastened using acupuncture needles.

The classification of cnidae follows den Hartog (1977) and England (1991), but nomenclature is based solely on England (1991). Thirty measurements (undischarged capsules) were taken from each cnida type out of each body region from two specimens of each species. The cnidome was analyzed under an Olympus BX53 compound microscope with phase contrast and Olympus image system. All parts of the body were analyzed separately so that any contamination was avoided. The two parts of mesenterial filaments (cnidoglandular tract and ciliated tract) were analyzed together using 30 measurements from each part. Each species name is formed as a noun in apposition to match the gender of the species with the gender of the genus.

## Taxonomy

Subclass Ceriantharia Perrier, 1893

Order Spirularia den Hartog, 1977

Family Cerianthidae

Milne Edwards & Haime, 1851

### Genus *Pachycerianthus* Roule, 1904

**Type species.** *Pachycerianthus multiplicatus* Carlgren, 1912 (see details in Kelly & Keegan, 2000).

**Diagnosis** (*sensu* Arai, 1965). Cerianthidae with second couple of protomesenteries short and sterile. Arrangement of mesenteries in each quartette M,B,m,b (1,3,2,4), more or less distinct.

**Distribution.** This genus is distributed worldwide.

### *Pachycerianthus delwynae* Carter, 1995

Fig. 1A–D

*Pachycerianthus delwynae* Carter, 1995: 2–3; figs 1b, 2.

*Pachycerianthus longistriatus* Carter, 1995: 3–4, junior synonym.

**Specimens examined.** Australian Museum (AM)—Australia, Sydney—G15399 (holotype of *P. delwynae*) Port Jackson, Chowder Bay, 33°50'30"S 151°15'12"E (15/ix/1989), depth 15 m; G15404 Port Jackson, Manly Pool, 33°50'S 151°17'E (1957); G14526, Port Jackson, Camp Cove, 33°50'S 151°16'E (2 specimens); G15808 Port Jackson, Vacluse Bay, 33°51'S 151°16'E (many specimens); G15400 (paratype of *P. delwynae*) Port Jackson, Bottle and Glass Rocks, 33°50'54"S 151°16'12"E (13/vii/1989), depth 5 m; G15401 (paratype of *P. delwynae*) Port Jackson, Bottle and Glass Rocks, 33°50'54"S 151°16'12"E (20/vii/1989), depth 7 m; G12555 (paratype of *P. longistriatus*) Port Jackson; G15403 (paratype of *P. longistriatus*) Port Jackson, Chowder Bay, 33°50'S 151°17'E; G12554 (paratypes of *P. longistriatus*) Port Jackson (09/1886) (5 specimens in jar but only 3 in good condition and only 3 cited by Carter (1995)); G15406 (paratypes of *P. longistriatus*) Port Jackson, Off Dawes Point, 33°50'S 151°12'E (2 specimens); G12553 (paratype of *P. longistriatus*) Port Jackson; G13558 (paratype of *P. longistriatus*) Port Jackson; G13561 (paratype of *P. longistriatus*) Port Jackson, G15405 (paratype of *P. longistriatus*) Port Jackson, Drummoyne (viii/1963); G15402 (holotype of *P. longistriatus*) Port Jackson, Taylors Bay, 33°50'S 151°17'E (20/vii/1989), depth 5 m.

**Remarks.** Closely related sympatric species always arouse much curiosity, especially regarding how the processes of speciation have occurred. However, the occurrence of two species of *Pachycerianthus* described from Sydney (Port Jackson) by Carter (1995) are not supported. Carter (1995) notes that separation of the two species based on anatomy is difficult because the differences in mesenterial organization are slight, but the external morphology, especially tentacle colouration, is more consistent with banded marginal tentacles in *P. delwynae* and with distinctive longitudinal

stripes on the marginals in *P. longistriatus*. However, colour patterns have been shown to be highly variable in Cnidaria, especially in Ceriantharia, where numerous examples of different colour morphs have been found to represent a single species when other characters are considered (e.g., Molodtsova *et al.*, 2011; Stampar *et al.*, 2012 (including molecular data); Stampar *et al.*, 2015). Some species have different colour morphs depending on the reproduction season that each polyp was produced (Stampar *et al.*, submitted), consequently, colour is not a reliable taxonomic character in Ceriantharia. Leaving aside tentacle colouration patterns, the two main anatomical features listed by Carter (1995) that differentiate the species are not consistent, presenting variations that overlap. The first of these is the arrangement of mesenteries. Carter (1995) indicates that in *P. delwynae* the M2 mesentery is longer than the M1 and indicates an opposite pattern in *P. longistriatus*, in which mesentery M2 is shorter than M1. Observing the same specimens studied by Carter (1995) it is possible to verify this pattern is only present in some individuals, in other specimens this pattern does not exist or is not as evident as described. However, two specimens (AM G12554 and AM G15405, both nominally paratypes of *P. longistriatus*) display a mixture of both morphological patterns; one side (from siphonoglyph to multiplication chamber) has mesenteries with the M2 longer than the M1, the other side has the inverse mesentery M1 is longer than the M2. The other character used to justify the separation into two species is the distribution of the insertion of the tentacles. This character is much more inconsistent than the form of the mesentery, at least four different arrangements occur. However, the most important aspect is that there is no difference in the number of pseudocycles of the tentacles of each type (marginal or labial) in all specimens. Therefore, it is not possible to keep these specimens as two separate species, *Pachycerianthus delwynae* is retained instead of *P. longistriatus* based on page precedence in Carter (1995).

### *Pachycerianthus fiordlandensis* sp. nov.

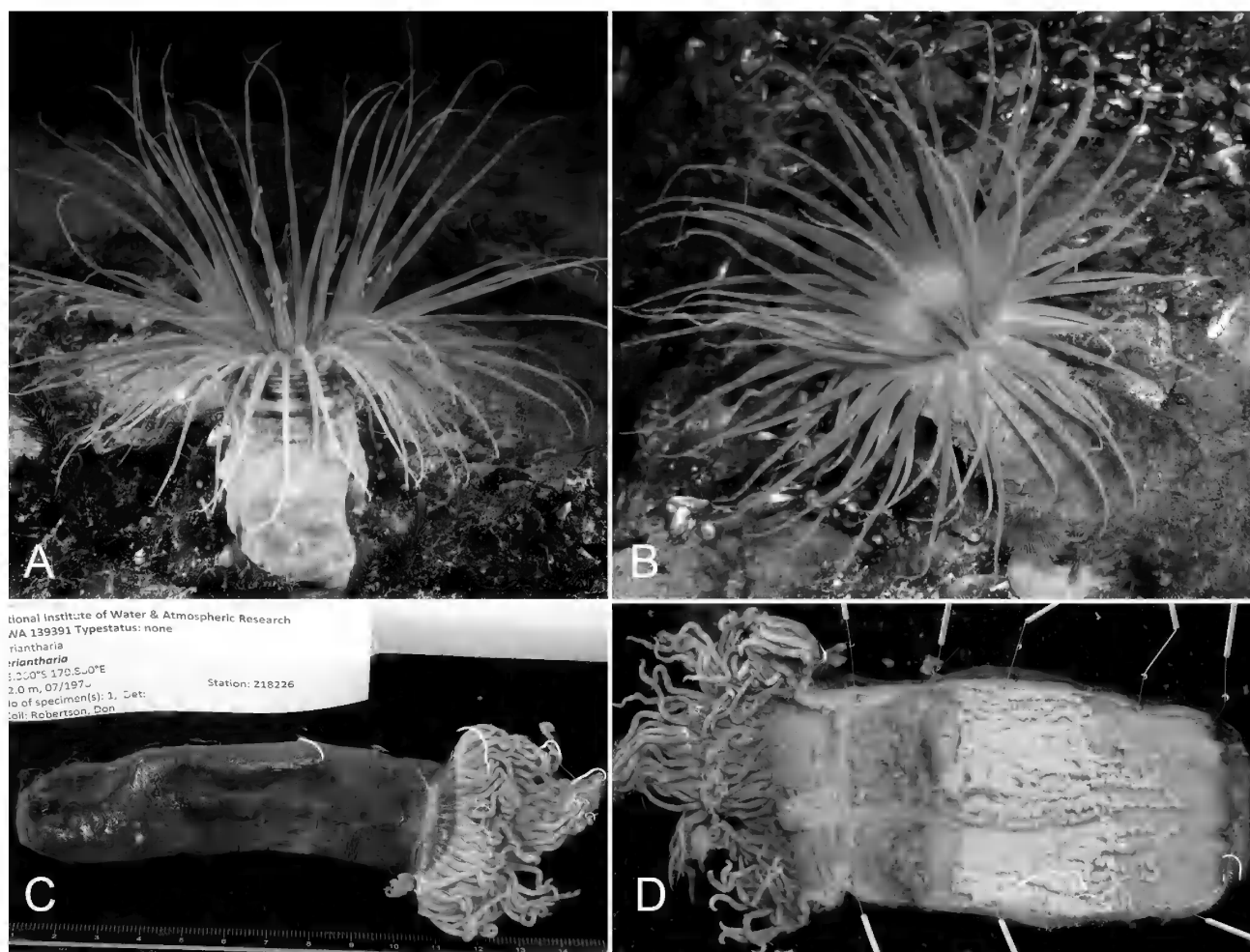
urn:lsid:zoobank.org:act:3653A1AC-810C-4A81-AFF1-85476384F369

Figs 2–4, Table 1

*Cerianthus bollonsi* Wing, 2003 (p. 247, in image caption); Wing, 2008 (p. 35 in image caption and p. 46), **nomen nudum**. (The name is cited, but there is no formal description of the species or designation of type material so it does not meet the criteria for acceptance as defined by the ICZN).

**Holotype.** NIWA Invertebrate Collection (NIC)—NIWA 139391 New Zealand, off Moeraki, Otago, 45.30°S 170.80°E (vii/1970), depth 82 m. **Paratypes.** New Zealand—NIWA 139397 Doubtful Sound, Fiordland, New Zealand Oceanographic Institution (NZOI) Station O869, 45.44°S 167.12°E (07/iii/1985), depth 5–35 m, (1 specimen); NIWA 139400 Milford Sound, Fiordland, NZOI Station W27, 44.66°S 167.91°E (13/xi/1985), depth 3–26 m, (1 specimen); NIWA 56235 Great Exhibition Bay, Northland, RV *Tangaroa* Station TAN0906/140, 34.57°S 173.20°E to 34.57°S 173.21°E (13/vii/2009), depth 117–120 m, (1 specimen); NIWA 35103 Milford Sound, Fiordland, 44.58°S 167.78°E (03/ix/1996), depth 20–25 m (3 specimens).





**Figure 2.** Specimens of *Pachycerianthus fiordlandensis* sp. nov. (A) Dusky Sound specimen, Fiordland, New Zealand, photo by Malcolm P. Francis; and (B) Milford Sound specimen, Fiordland, NZ, photo by Chris Woods; (C, D) holotype, NIWA 139391.

**Diagnosis.** Marginal tentacles brown to light brown. Six mesenteries attached to siphonoglyph, very long P2 mesentery, long m mesenteries and presence of directive labial tentacle.

**Variation.** Slightly long (up to 110 mm long) and thin (20–25 mm width) cerianthid; 60–88 brown to light brown (Fig. 1) marginal tentacles (110–120 mm in preserved specimens), arrangement 1243.2314.2314..., with more than 6 pores per tentacle, 56–72 dark brown labial tentacles (up to 50 mm long in preserved specimens), arrangement (2)312.1321.3213..., unpaired labial tentacle present; pleated stomodeum extending over 1/4 of total body length, hyposulcus 4–6 mm long, hemisulci distinct; siphonoglyph rather narrow, connected to directives, P2 and P3 (6 mesenteries); free parts of sterile directive mesenteries 1/3 of length of siphonoglyph, without mesenterial filaments. Second protomesenteries long, 2/3 of gastral cavity, fertile, bearing ciliated tracts with bundles of craspedonemes, with short (1/5 of mesentery length) cnido-glandular tract and long (~90% of the mesentery) craspedion tract. Third protomesenteries sterile, three times longer than directives, with short craspedonemes. M and m-mesenteries long, fertile; M1 and M2 reaching almost aboral pore (M2 shorter than M1), with bundles of craspedonemes; B and b-mesenteries, sterile, B longer than

b; see Fig. 3 for schematic arrangement of mesenteries. The cnidome of the species (Fig. 4) is composed of spirocysts, atrichs, microbasic b-mastigophores (four types) and ptychocysts distributed as shown in Table 1.

**Holotype description** (NIWA 139391). Somewhat elongated polyp, 9.6 cm long, 25 mm diameter just below marginal tentacles and 20 mm near aboral end. Marginal tentacles 88, arranged in four pseudocycles, 110–120 mm long and 2 mm in diameter near the base, light brown. The space between cycles of marginal and labial tentacles brown colored. Labial tentacles 72, about 50 mm long, dark brown, directive labial present, arrangement of marginal tentacles 1243.2314.2314... and labial tentacles (2)312.1321.3213... Oral disk 25 mm wide, stomodeum 24 mm long, dark brown, siphonoglyph narrow and elongate with 6 mesenteries attached, hyposulcus 3 mm long with short hemisulci 1.5 mm long. Free parts of directive mesenteries without mesenterial filaments. Second protomesenteries with 2/3 of gastral cavity, fertile, bearing ciliated tract with bundles of craspedonemes. Third protomesenteries sterile, three times longer than directives, with short craspedonemes. M1 and M2 reaching almost aboral pore (M2 shorter than M1), with bundle of craspedonemes; B and b-mesenteries, sterile, B longer than b.

**Table 1.** Cnidome of *Pachycerianthus fiordlandensis* sp. nov. based on two specimens (NIWA 139391; 139400). Mean and range given for each cnida.

| <i>Pachycerianthus fiordlandensis</i> sp. nov. |                            |                           |
|--|----------------------------|---------------------------|
|  | length (in $\mu\text{m}$ ) | width (in $\mu\text{m}$ ) |
| column   |                            |                           |
| pytchocysts                                    | 63.7 (55.7–71.2)           | 18.5 (14.5–22.2)          |
| atrachs  | 32.5 (26.2–41.5)           | 6.85 (5.1–8.2)            |
| b-mastigophores ii                             | 32.1 (29.5–34.5)           | 6.6 (5.4–7.3)             |
| b-mastigophores iv                             | 14.8 (12.6–15.7)           | 3.5 (3.1–3.9)             |
| marginal tentacles                             |                            |                           |
| b-mastigophores i                              | 36.5 (34.6–37.5)           | 6.2 (5.6–6.9)             |
| b-mastigophores ii                             | 31.5 (29.5–33.8)           | 6.5 (5.8–7.2)             |
| atrachs  | 33.5 (31.5–36.5)           | 6.6 (5.6–7.6)             |
| labial tentacles                               |                            |                           |
| b-mastigophores i                              | 36.8 (34.9–37.6)           | 6.2 (5.8–6.8)             |
| b-mastigophores iii                            | 17.7 (15.8–18.9)           | 4.5 (3.9–5.3)             |
| atrachs  | 33.4 (31.5–36.2)           | 6.5 (5.5–7.7)             |
| stomodeum                                      |                            |                           |
| b-mastigophores i                              | 36.5 (33.9–37.8)           | 5.9 (5.2–6.7)             |
| b-mastigophores ii                             | 30.8 (29.1–31.9)           | 6.3 (5.8–6.4)             |
| atrachs  | 31.3 (28.8–33.5)           | 5.9 (5.1–6.9)             |
| mesenteries Type b                             |                            |                           |
| b-mastigophores ii                             | 30.5 (29.1–32.1)           | 6.3 (5.8–6.4)             |
| atrachs  | 33.1 (30.1–33.8)           | 6.4 (5.7–6.8)             |
| mesenteries Type m                             |                            |                           |
| b-mastigophores ii                             | 31.2 (29.8–32.3)           | 6.4 (5.9–6.7)             |
| atrachs  | 31.9 (30.1–32.5)           | 6.1 (5.5–6.6)             |

**Remarks.** Specimens of this species have previously been recorded in photographs by divers (Fig. 2A,B) and discussed in some general books on marine biodiversity for the coastal region of New Zealand (e.g., Cairns *et al.*, 2009; Grange *et al.*, 1981 (as *Cerianthus* sp.); Grange & Brook, 2010; Wing, 2003, 2008 [as *Cerianthus bollonsi*]). It is noted by divers for its long flowing tentacles and very rapid “disappearing act” when disturbed (Francis, pers. comm.; Wing, 2008). The species ranges from shallow areas from about 15 m to around 100 m deep. This wide range is not very common in Ceriantharia, except for a few species such as *Ceriantheopsis americana* and *Pachycerianthus borealis* (Shepard *et al.*, 1986). It is usually found in an upright position with its tube buried in coarse sediments or shell hash on sand slopes or sediment filled ledges in the deep rock wall zones in the fiords (Grange *et al.*, 1981; Wing, 2003; Woods, pers. comm.). All specimens had well developed gonads with deep orange oocytes. This has also been observed in other species of the genus, such as *Pachycerianthus schlenzae* (Stampar *et al.*, 2014) and may be linked to high levels of egg yolk.

**Distribution.** New Zealand and adjacent areas (from shallow waters to 120 m).

**Etymology.** The specific name “*fiordlandensis*” is based on the area of occurrence, Fiordland, New Zealand, in which specimens are commonly observed.

### *Pachycerianthus antarcticus* sp. nov.

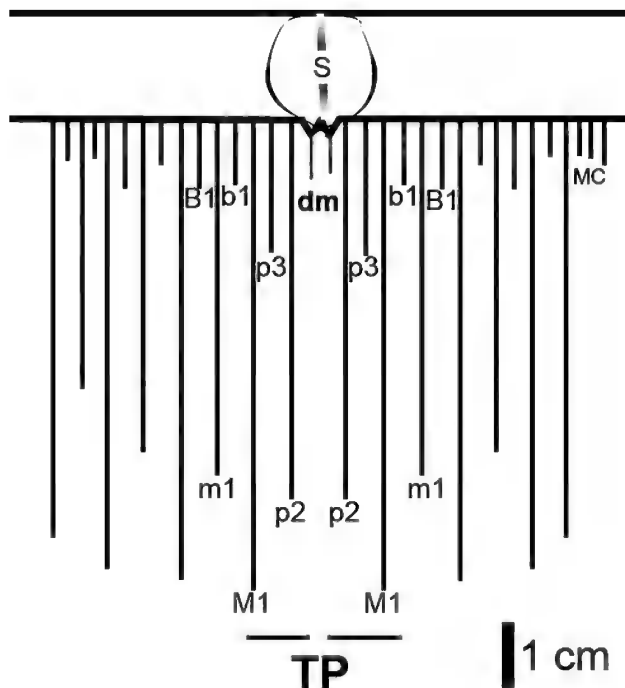
urn:lsid:zoobank.org:act:E206225A-DAFB-44AE-A59E-FE1D7651F5E2

Figs 5–7, Table 2

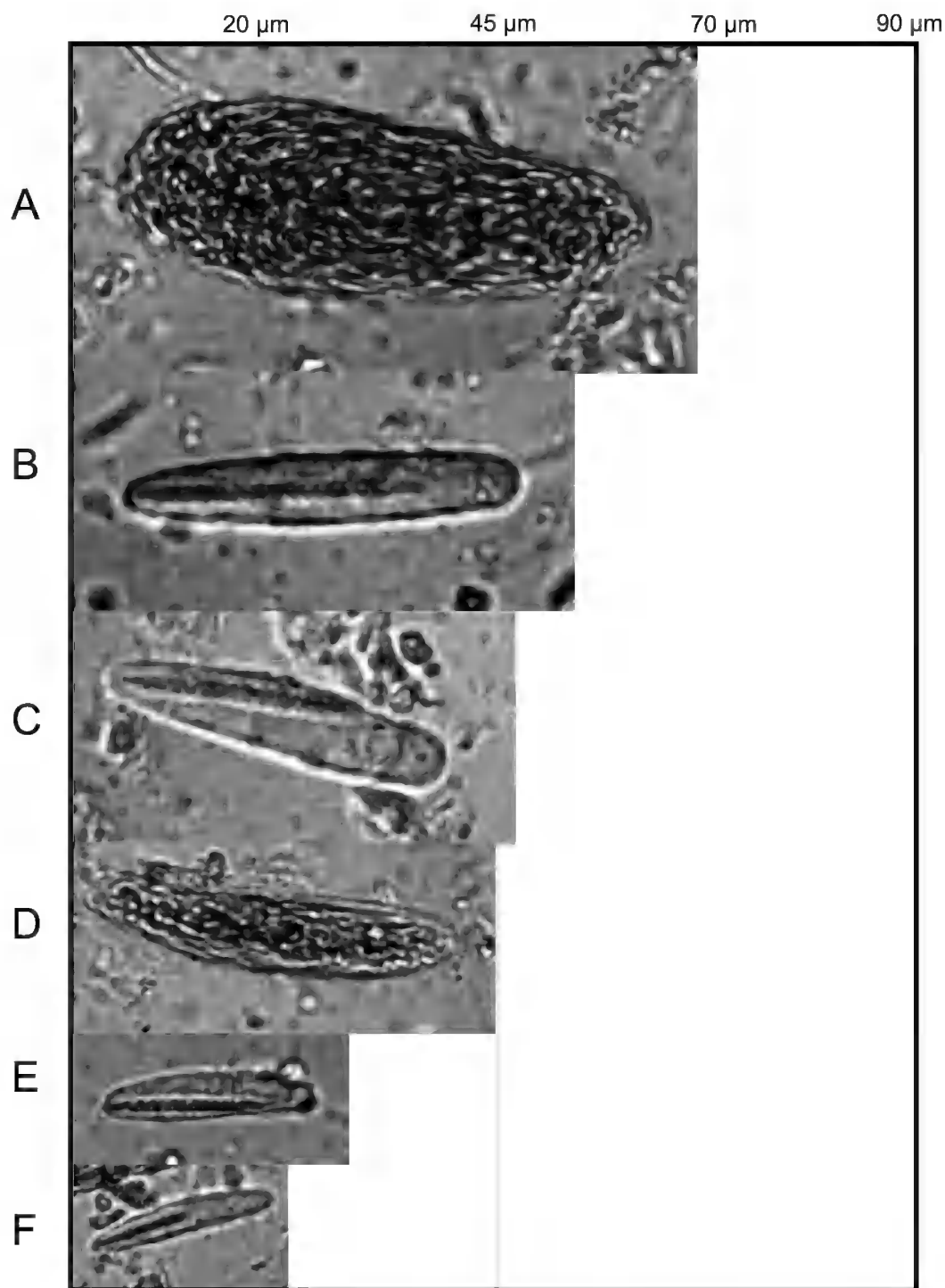
**Holotype.** NIWA Invertebrate Collection (NIC) NIWA 36894 Ross Sea, Antarctica, RV *Tangaroa* Station TAN0802/100, 76.2020°S 176.2480°E (18/ii/2008), depth 447–451 m. **Paratype.** NIWA 103267 Off Young Island, Antarctica, RV *Tangaroa* Station TAN0402/252, 66.3647°S 162.5762°E (05/iii/2004), depth 942 m (1 specimen).

**Diagnosis.** Marginal tentacles in two pseudocyles and labial tentacles in four pseudocycles. Four mesenteries attached to siphonoglyph, M and m or B and b with almost the same length and absence of directive labial tentacle.

**Variation.** Short (up to 36 mm long) and broad (10 mm width) cerianthid; 20–32 white marginal tentacles (practically absent in both specimens, only the base is present) (Fig. 4), arrangement 1212.1212.1212; 28–36 white tentacles (up to 4 mm long in preserved specimens), arrangement 2134.3142.3142, unpaired labial tentacle absent; pleated stomodeum extending over 1/5 of total body length, hyposulcus less than 1 mm long, hemisulci absent; siphonoglyph narrow, connected only to directives and P2 (4 mesenteries); free parts of sterile directive mesenteries very short, without mesenterial filaments. Second protomesenteries (P2) short, sterile, bearing ciliated tracts without craspedonemes, followed by a long cnido-glandular tract (c. 80% of the mesentery). Third protomesenteries sterile, longer than P2, with craspedonemes. M and m-mesenteries long, almost equal length (M longer than m), fertile; M1 and M2 reach more than 1/2 of gastral cavity with a small bundle of craspedonemes; B and b-mesenteries, short, sterile, almost equal length; see Fig. 6 for schematic



**Figure 3.** Graphical representation of the arrangement of mesenteries of *Pachycerianthus fiordlandensis* sp. nov. Abbreviations: M.C., multiplication chamber; dm, directives; T.P., terminal pore; S, siphonoglyph; B, betamesenteries (convoluted mesentery); M, metamesenteries (double filament); P, protomesenteries.

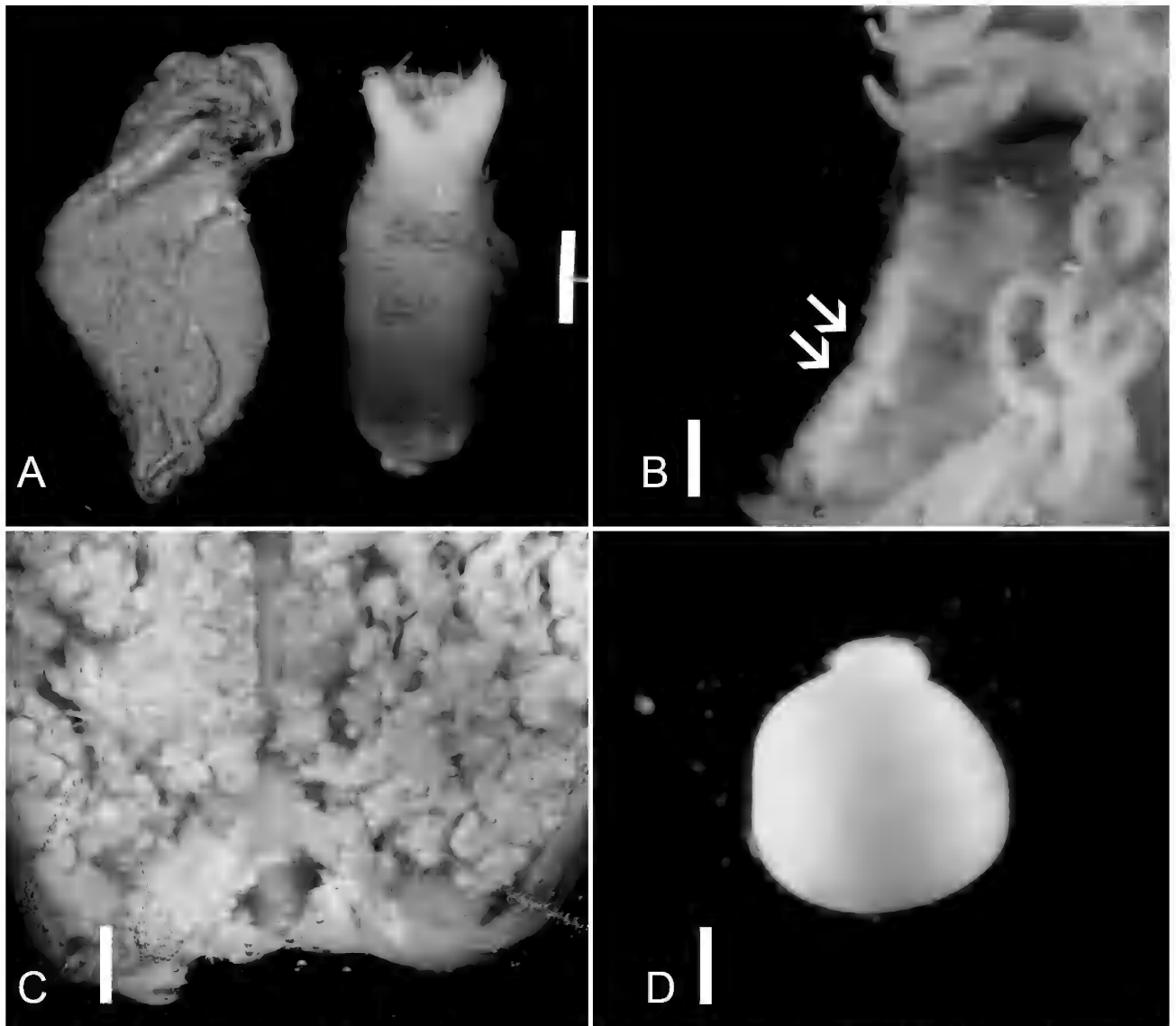


**Figure 4.** Cnidome of *Pachycerianthus fiordlandensis* sp. nov. based on two specimens (NIWA 139391; 139400).

arrangement of mesenteries. The cnidome of the species (Fig. 7) is composed of spirocysts, holotrics, atrichs, microbasic b-mastigophores (four types) and ptychocysts distributed as shown in Table 2.

**Holotype description** (NIWA 36894). Small polyp, 3.6 cm long, 11 mm diameter just below marginal tentacles and 4 mm near aboral end. Marginal tentacles 20, arranged in two pseudocycles. The space between cycles of marginal and labial tentacles white. Labial tentacles 28, about 3

mm long, white, directive labial absent, arrangement of marginal tentacles 1212.1212.1212... and labial tentacles 2134.3142.3142... . Oral disk 11 mm wide, stomodeum 6 mm long, white, siphonoglyph narrow and elongate with 4 mesenteries attached, hyposulcus 2 mm long with short hemisulci 1 mm long. Free parts of directive mesenteries very short, without mesenterial filaments. Second protomesenteries short, sterile, bearing small ciliated tracts with bundles of craspedonemes. Third protomesenteries sterile, short, with craspedonemes. M and



**Figure 5.** Specimens of *Pachycerianthus antarcticus* sp. nov. (A) Whole specimen with tube, NIWA 36894, holotype (photo: Stefano Schiaparelli, MNA Genoa, IPY-CAML); (B) detail of insertion area of marginal tentacles (arrows); (C) detail of mesenteries full of eggs; and (D) eggs (fertilized?).

m-mesenteries long and almost equal length, fertile; M1 and M2 reaching almost aboral pore (M1=M2), with bundles of craspedonemes; B and b-mesenteries sterile, B two times longer than b.

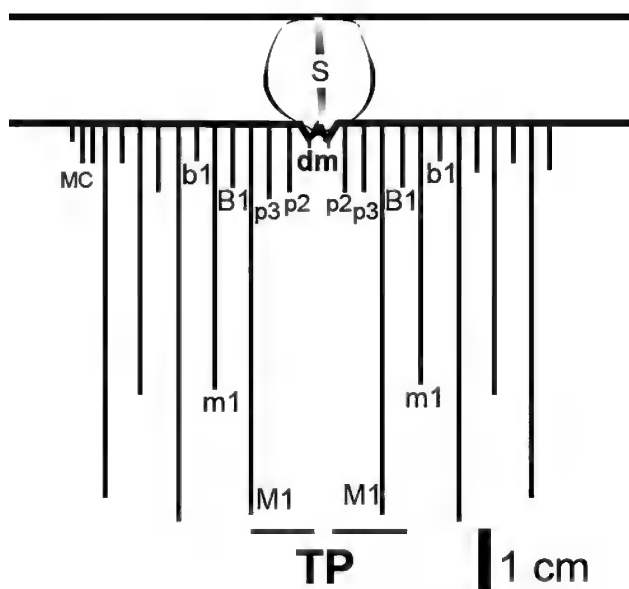
**Remarks.** *Pachycerianthus antarcticus* is the first species of Ceriantharia to be recorded for the Antarctic region. In contrast to the pattern of species occurrence in the Arctic, records in the southern hemisphere have previously been restricted to semitropical or temperate regions (e.g., Molodtsova *et al.*, 2011; Stampar *et al.*, 2014).

Some aspects related to the species biology are important to highlight. The first is the presence of oocytes that appear to be fertilized in the gastrovascular cavity. Internal fertilization is not unknown in Ceriantharia (Nyholm, 1943), but appears to be rare and there is no data on the fertilization process. Presently it is unclear if self-fertilization or oral sperm capture occurs. Another aspect concerns the size of

the ptychocyst capsules and the tube construction. Based on the small pieces of tube close to the specimen body, it is possible to observe a coarse grain size in the sediment used, so the construction of the tube must require longer ptychocyst filaments to be able to use this sediment as part of the tube (Stampar *et al.*, 2015). Based on current data, no further conclusions are possible, but a deeper analysis of the relationship between ptychocyst capsule size and sediment particle size would be useful to examine in future studies because the ecological role of these organisms can be quite important in modifying benthic environments (e.g., Shepard *et al.*, 1986).

**Distribution.** Southern Ocean, Antarctica.

**Etymology.** The specific name “antarcticus” (derived from the ancient Greek ἀνταρκτικός opposite to the Arctic) refers to the geographical occurrence of the specimens.



**Figure 6.** Graphical representation of the arrangement of mesenteries of *Pachycerianthus antarcticus* sp. nov. Abbreviations: *M.C.*, multiplication chamber; *dm*, directives; *T.P.*, terminal pore; *S*, siphonoglyph; *B*, betamesenteries (convoluted mesentery); *M*, metamesenteries (double filament); *P*, protomesenteries.

**Table 2.** Cnidome of *Pachycerianthus antarcticus* sp. nov. based on two specimens (NIWA 36894 and 103267). Mean and range given for each cnida.

| <i>Pachycerianthus antarcticus</i> sp. nov. |                            |                           |
|---|----------------------------|---------------------------|
|   | length (in $\mu\text{m}$ ) | width (in $\mu\text{m}$ ) |
| column                                      |                            |                           |
| pytchocysts                                 | 59.9 (53.5–65.2)           | 16.5 (14.5–19.2)          |
| holotrich                                   | 64.5 (59.5–69.3)           | 18.2 (14.5–19.2)          |
| atrichs                                     | 36.4 (32.5–40.5)           | 8.2 (5.1–9.9)             |
| b-mastigophores ii                          | 29.5 (27.7–33.5)           | 6.9 (5.8–7.7)             |
| b-mastigophores iii                         | 26.8 (23.9–27.9)           | 7.6 (6.5–8.6)             |
| marginal tentacles                          |                            |                           |
| b-mastigophores iv                          | 18.7 (75.6–92.3)           | 6.1 (5.4–6.9)             |
| atrichs                                     | 32.6 (31.7–36.6)           | 7.2 (6.6–7.9)             |
| labial tentacles                            |                            |                           |
| b-mastigophores i                           | 86.7 (75.6–92.3)           | 10.1 (8.9–11.7)           |
| b-mastigophores ii                          | 29.4 (26.3–32.9)           | 6.6 (5.7–7.5)             |
| atrichs                                     | 38.5 (34.1–40.6)           | 8.3 (5.5–10.2)            |
| stomodeum                                   |                            |                           |
| b-mastigophores i                           | 84.5 (72.5–89.6)           | 9.8 (8.5–10.9)            |
| b-mastigophores ii                          | 28.6 (27.1–29.9)           | 6.6 (6.2–7.2)             |
| atrichs                                     | 30.7 (29.2–32.5)           | 7.9 (7.1–8.6)             |
| mesenteries Type b                          |                            |                           |
| atrichs                                     | 30.9 (29.4–33.2)           | 8.1 (6.9–9.2)             |
| mesenteries Type m                          |                            |                           |
| b-mastigophores ii                          | 30.8 (29.2–33.1)           | 6.7 (6.2–7.3)             |

## *Pachycerianthus nobilis* (Haddon & Shackleton, 1893)

*Cerianthus nobilis* Haddon & Shackleton, 1893: 116, 118; Carlgren, 1896: 174; Haddon, 1898: 400–401; Pax, 1910: 167.

*Pachycerianthus nobilis* Molodtsova, 2000: 19; Molodtsova, 2007: 133; Stampar *et al.*, 2014: 350, 352.

**Specimens examined.** AM G16074, Dunwich, Stradbroke Island, Moreton Bay, Queensland, Australia, 27.50°S 153.40°E (1974); AM G18351, Dunwich, Stradbroke Island, Moreton Bay, Queensland, Australia (06/viii/1961), on sand flats (5 specimens); Museum and Art Gallery of the Northern Territory: NTM CO14354, Town Hall, Channel Island, Darwin Harbor, Darwin, Northern Territory, Australia, 12.550°S 130.833°E, 6–8 m depth.

**Remarks.** The specimens studied come from southern Queensland and the northern part of the Northern Territory. As this species has been described from Torres Strait in northern Queensland, the distribution appears to be quite broad, encompassing the Timor Sea, Arafura Sea and Coral Sea. The polyps generally have a whitish-green color in the tentacle region and reddish-brown color in the column. However, some live specimens have different tentacle colors, including purple to green marginal tentacles. All specimens examined were fertile, including those smaller than 3 cm in length. This indicates that reproductive maturity is reached rapidly and long before specimens reach the maximum reported size for the species (10 cm in preserved specimens). This is a very little studied species but is apparently common and of commercial importance as it is sold in aquarium stores to amateur hobbyists (SNS personal observation). Therefore, an assessment of conservation status and reproductive patterns of this species would be valuable.

**Distribution.** Queensland and Northern Territory, Australia, New Caledonia, depth: shallow waters.

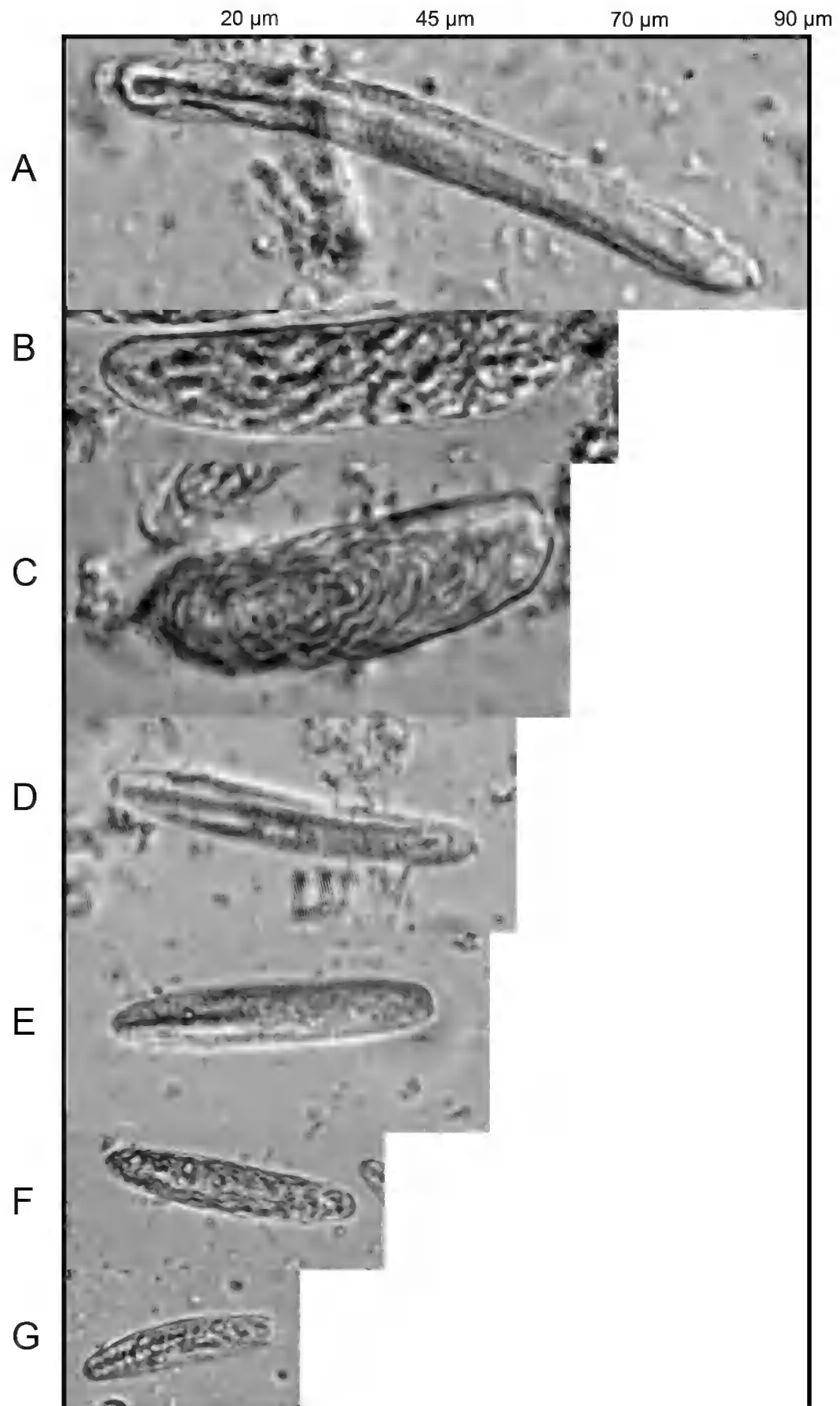
## Genus *Ceriantheopsis* Carlgren, 1912

**Type species.** *Ceriantheopsis americana* (Agassiz in Verrill, 1864) by subsequent designation (Carlgren, 1912, p. 24).

**Diagnosis.** Cerianthids with alternating sterile and fertile mesenteries. Second protomesenteries fertile, reaching aboral pole. Metamesenteries arranged in mBMB. Length of all but M-metamesenteries diminishes toward multiplication chamber. Length of M-metamesenteries of first 2–4 quartets can increase toward the multiplication chamber. M3 and further mesenteries can diminish in length towards multiplication chamber (Carlgren, 1912).

**Distribution.** Previously restricted to the Atlantic Ocean (Caribbean Sea, Gulf of Mexico, US Coast and South Africa Coast), expanded in this study to the South Pacific with the description of a new species.





**Figure 7.** Cnidome of *Pachycerianthus antarcticus* sp. nov. based on the holotype.

*Ceriantheopsis microbotanica* sp. nov.

urn:lsid:zoobank.org:act:965A7558-90F3-4061-AA9C-9C3C8DA0BDFE

Figs 8–10, Table 3

**Holotype.** Australian Museum G18354, Botany Bay, west of Port Botany, New South Wales, Australia 33.98°S 151.20°E (13/ii/1975), depth not recorded. **Paratypes.** Botany Bay, New South Wales, Australia (12/x/1995), all Smith-McIntyre grab, AM G18356, 33.97°S 151.19°E, 15.5 m (1 specimen), AM G18357, 33.97°S 151.18°E, 16.3 m (2 specimens), AM G18358 33.96°S 151.18°E, 16.3 m (1 specimen).

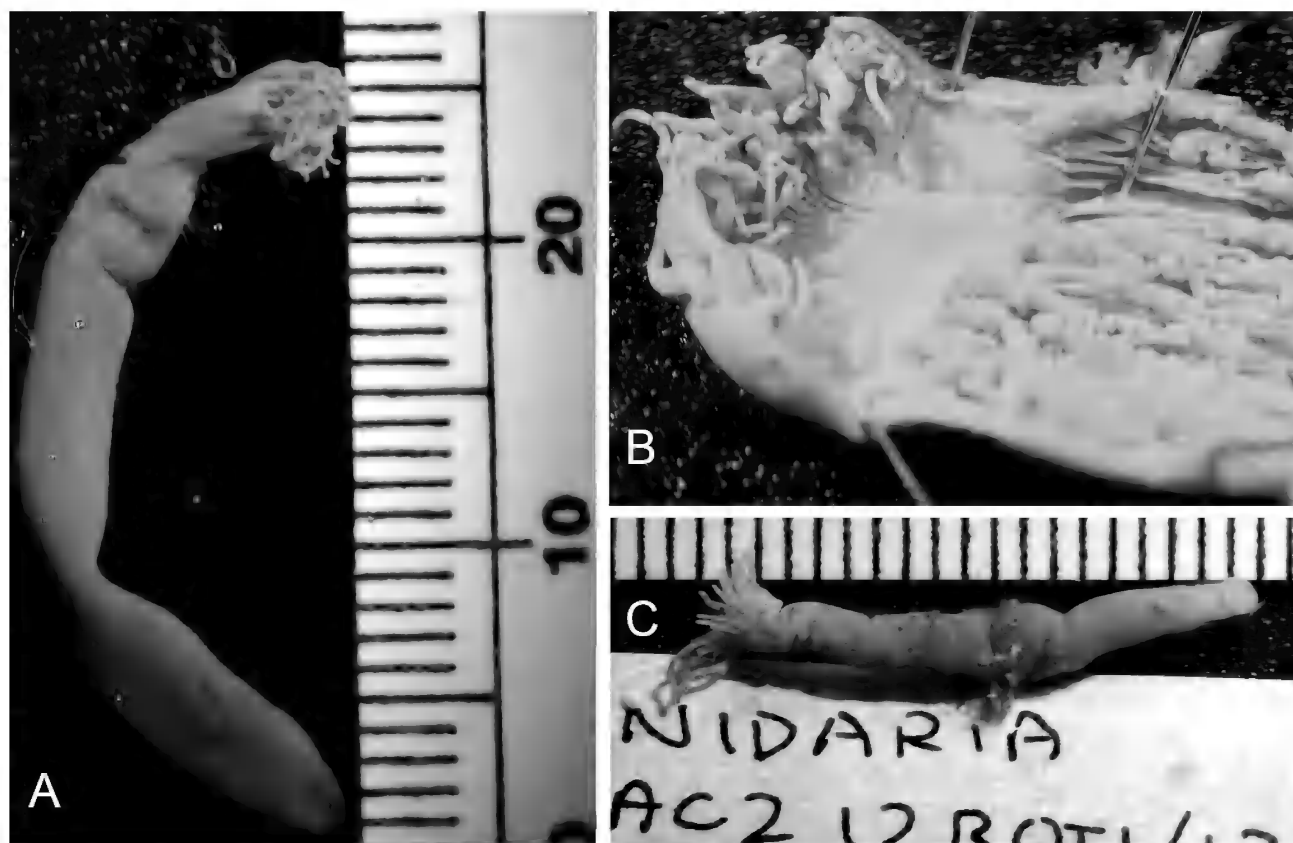
**Diagnosis.** Labial tentacles in two pseudocycles. Only directive mesenteries attached to siphonoglyph, presence of directive labial tentacle, M and m mesenteries with almost same length and very short mesenterial structures.

**Variation.** Elongated (up to 40 mm long) and narrow (3–4 mm width) cerianthid; 20–38 brown marginal tentacles (3–4 mm in preserved specimens), arrangement 1212.1212.1212..., no visible pores on tentacle; 16–36 brown labial tentacles (up to 2 mm long in preserved specimens), arrangement (2)131.3212.3212..., unpaired labial tentacle present; slightly smooth stomodeum extending over 1/6 to 1/7 of total body length, hyposulcus 2 mm long, hemisulci 1 mm long; siphonoglyph narrow, connected only to directives; free parts of sterile directive mesenteries almost the half length of siphonoglyph, without mesenterial filaments. Second protomesenteries almost reaching aboral pole, fertile, with very short cnido-glandular tracts (c. 20% of the mesentery). Third protomesenteries sterile, longer

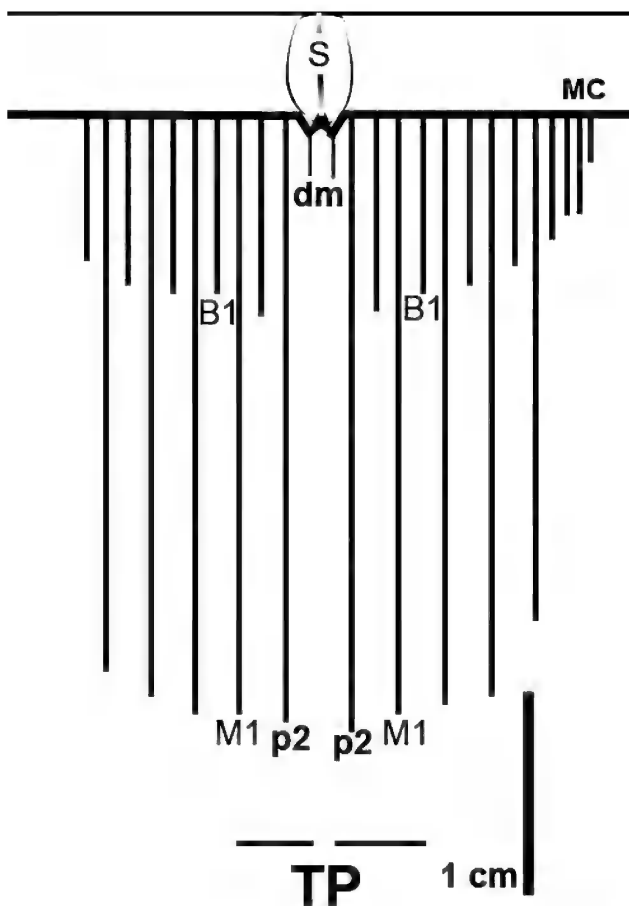
than 1/4 of P2, with craspedonemes at middle region. M and m-metamesenteries long, fertile; M1 and m1 almost reach aboral pore with bundles of craspedonemes and cnido-glandular tracts (c. 30% of the mesentery); B and b-mesenteries, sterile, B mesenteries 30% longer than b; see Fig. 9 for schematic arrangement of mesenteries. The cnidome of the species (Fig. 10) is composed of spirocysts, microbasic b-mastigophores (three types) and ptychocysts distributed as shown in Table 3.

**Table 3.** Cnidome of *Ceriantheopsis microbotanica* sp. nov. based on two specimens (AM G18354 and AM G18358). Mean and range given for each cnida.

| <i>Ceriantheopsis microbotanica</i> sp. nov. |                            |                           |
|--|----------------------------|---------------------------|
|  | length (in $\mu\text{m}$ ) | width (in $\mu\text{m}$ ) |
| column                                       |                            |                           |
| ptychocysts                                  | 52.5 (49.6–58.2)           | 18.5 (16.5–22.2)          |
| b-mastigophores i                            | 42.6 (36.8–45.5)           | 9.2 (8.7–10.1)            |
| atrachs                                      | 41.5 (36.5–44.5)           | 8.9 (7.6–9.9)             |
| marginal tentacles                           |                            |                           |
| b-mastigophores i                            | 41.5 (36.9–43.7)           | 9.1 (8.5–9.9)             |
| b-mastigophores ii                           | 16.5 (12.5–19.4)           | 7.2 (6.6–7.9)             |
| labial tentacles                             |                            |                           |
| b-mastigophores ii                           | 16.7 (13.2–18.2)           | 7.6 (6.8–7.9)             |
| stomodeum                                    |                            |                           |
| b-mastigophores ii                           | 16.4 (12.8–17.6)           | 7.3 (6.5–8.1)             |
| mesenteries Type m                           |                            |                           |
| b-mastigophores iii                          | 11.2 (9.4–12.1)            | 3.7 (3.2–4.3)             |



**Figure 8.** Specimens of *Ceriantheopsis microbotanica* sp. nov. (AM G18357). (A, C) Whole specimens; (B) detail of siphonoglyph.



**Figure 9.** Graphical representation of the arrangement of mesenteries of *Ceriantheopsis microbotanica* sp. nov. Abbreviations: Abbreviations: *M.C.*, multiplication chamber; *dm*, directives; *T.P.*, terminal pore; *S*, siphonoglyph; *B*, betamesenteries (convoluted mesentery); *M*, metamesenteries (double filament); *P*, protomesenteries.

**Holotype description** (AM G18354). Elongated polyp, 38 mm long, 4 mm diameter just below marginal tentacles and 3 mm near aboral end. Marginal tentacles 38, arranged in two pseudocycles, 3–4 mm long and 0.5 mm in diameter near the base, brown with a lighter longitudinal line. The space between cycles of marginal and labial tentacles short and light brown. Labial tentacles 36, arranged in four pseudocycles, about 2 mm long, brown, directive labial present, arrangement of marginal tentacles 1212.1212.1212... and labial tentacles (2)131.3212,3212... Oral disk 4 mm wide, stomodeum 5 mm long, light brown, siphonoglyph narrow and elongate with 2 mesenteries attached (directives), hyposulcus 1.7 mm with short hemisulci 0.7 mm long. Free parts of directive mesenteries rather short, without mesenterial filaments. Second protomesenteries almost reach aboral pole, fertile, bearing ciliated tract at first 1/4 of the mesentery. Third protomesenteries sterile, longer than 1/4 of the P2, with craspedonemes at first 1/4 of the mesentery. M and m-metamesenteries indistinct with the same length, fertile; M1 and m1 almost reach the aboral pore (9/10 of gastral cavity) with mesenteric filaments at first 1/4 of each mesentery; B mesenteries 30% longer than b mesenteries.

**Remarks.** This species has a very unusual form, probably due to the small body size. The organization of the mesentery seems to have been restricted and it is not possible to verify a clear difference between the same type of mesenteries, B or M. Still, the genus *Ceriantheopsis* is the most suitable placement for this species, because of the mesenterial arrangement (with long and fertile P2). This species is unusual because of its small size and also seems endemic to a very restricted area. All specimens were collected in benthic surveys. In one of these studies, two estuaries, Botany Bay and Pittwater, were evaluated for comparative purposes with many samples (Wilson *et al.*, 1998). The distance between these two regions is only 50 km. Interestingly, samples of *Ceriantheopsis microbotanica* only come from Botany Bay. Perhaps there is some strong biological or other reason that has restricted collections to date to this location. This is also potentially a very interesting species for studies of evolutionary developmental mechanisms (evo-devo) because its small size can be compared with the well-known biological model *Nematostella vectensis* (Darling *et al.*, 2005; He *et al.*, 2019).

**Distribution.** Botany Bay, Sydney, Australia.

**Etymology.** The species name is derived from a mixture of the locality name (Botany Bay) and the size of the specimens (micro).

### *Ceriantheopsis zealandiaensis* sp. nov.

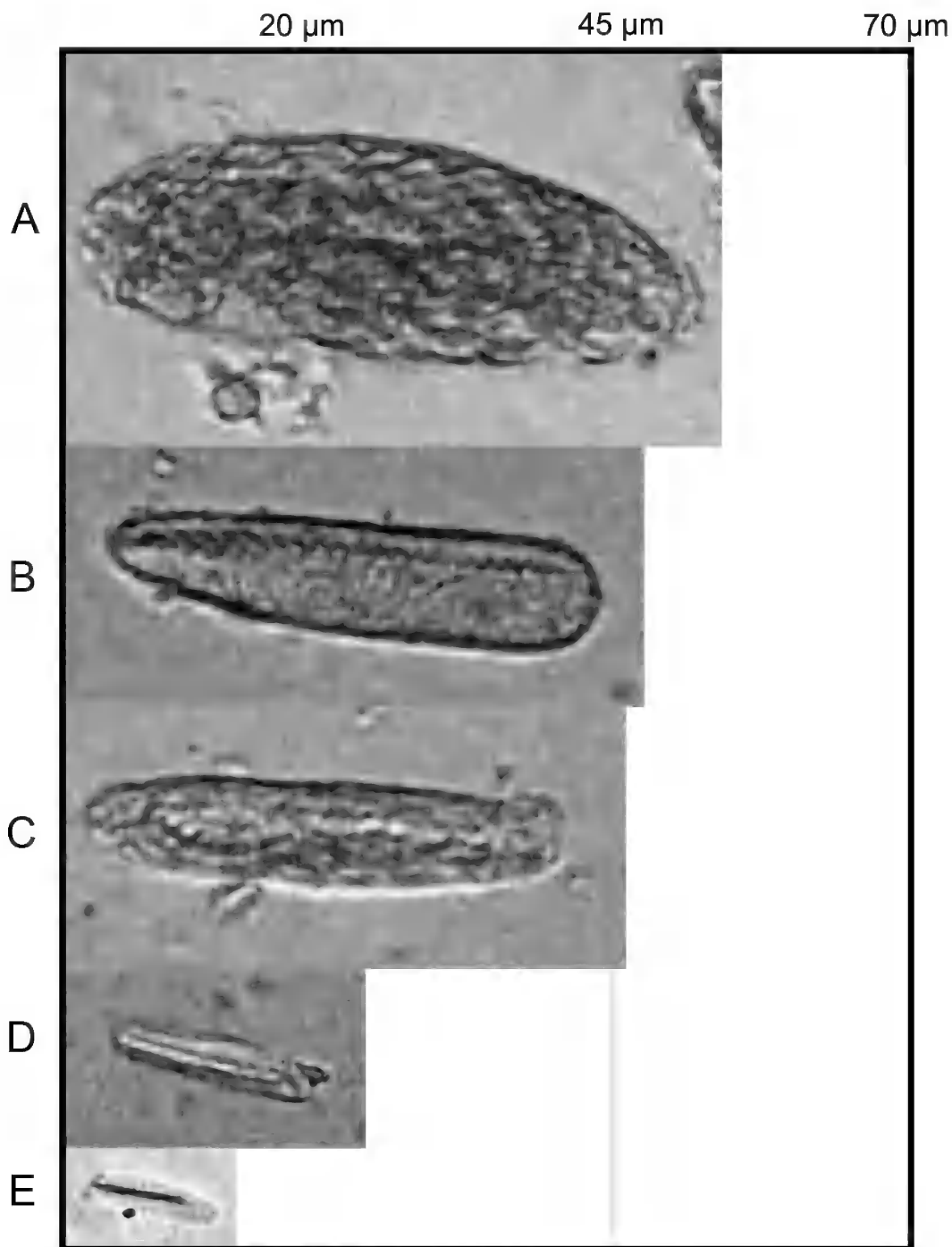
urn:lsid:zoobank.org:act:BC26F829-165B-4AA4-B4CF-0AF6673C72E7

Figs 11–13, Table 4

**Holotype.** NIWA Invertebrate Collection (NIC), NIWA 87139, Gaer Arm, Whale Rock, Fiordland, 45.2825°S 167.1211667°E (19/ii/2013), depth c. 15 m. **Paratype.** NIWA 145027, same details as holotype.

**Diagnosis.** Labial tentacles dark brown. Eight mesenteries attached to siphonoglyph, P2 with 3/4 of gastral cavity, labial tentacles in three rows.

**Variation.** Long (up to 150 mm long) and thin (10–20 mm width) cerianthid; 64–70 light brown marginal tentacles (20–22 mm in preserved specimens), at least one line over marginal tentacle length, arrangement 3412.3412.3412, with more than 6 pores per tentacle; 56–62 dark brown labial tentacles (up to 07 mm long in preserved specimens), arrangement (2)313.2123.2123, unpaired labial tentacle present; pleated stomodeum extending over 1/6 to 1/7 of total body length, hyposulcus 3 mm long, hemisulci distinct; siphonoglyph wide, connected to four pairs of mesenteries; free parts of sterile directive mesenteries shorter than siphonoglyph length, without mesenterial filaments. Second protomesenteries almost reaching aboral pole with 3/4 of gastral cavity, fertile, bearing ciliated tracts with bundles of craspedonemes at the very beginning, followed by very short cnido-glandulars tract and long (c. 90% of the mesentery) craspedion tracts. Third protomesenteries sterile, longer than B1 and much longer than directives, with craspedonemes. M and m-metamesenteries long, fertile; M1 reach 3/5 of total body length and M2 reaching almost the same, but shorter than M1, with bundles of craspedonemes; B and b-mesenteries, sterile, with B almost twice length of b;

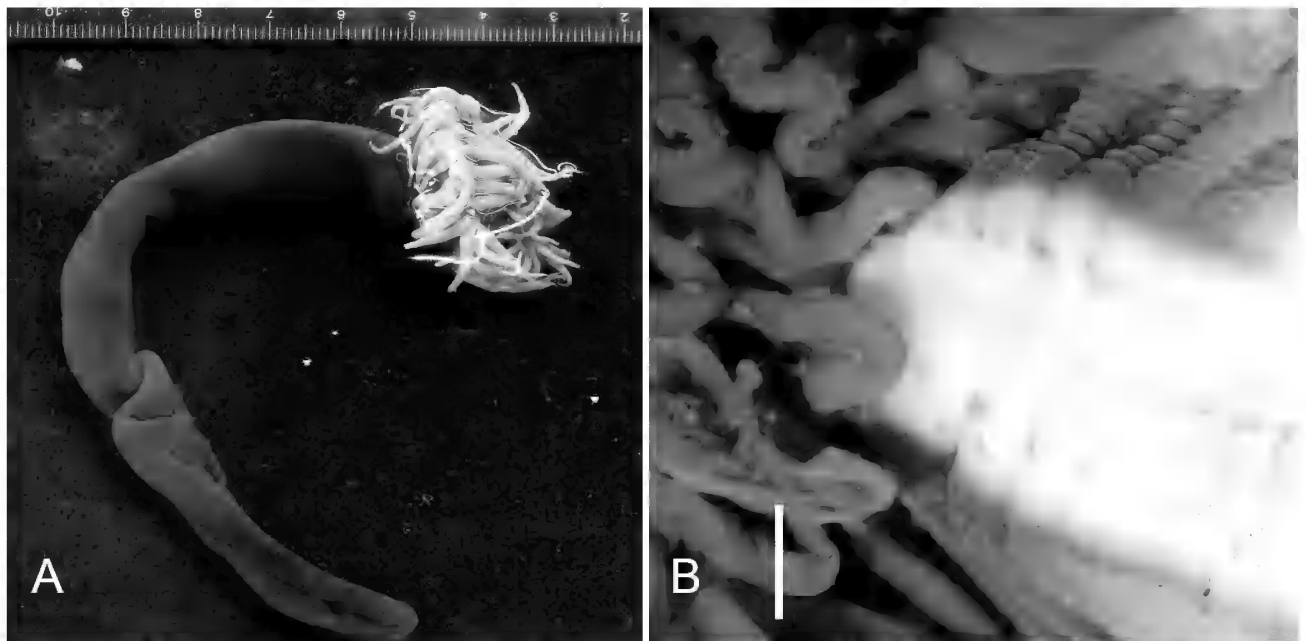


**Figure 10.** Cnidome of *Ceriantheopsis microbotanica* sp. nov. based on two specimens (AM G18354 and AM G18358).

see Fig. 12 for schematic arrangement of mesenteries. The cnidome of the species (Fig. 13) is composed of spirocysts, holotrichs, microbasic b-mastigophores (three types) and ptychocysts distributed as shown in Table 4.

**Holotype description** (NIWA 87139). Rather elongated polyp, 7 cm long, 19 mm diameter just below marginal tentacles and 7 mm near aboral end. Marginal tentacles 64, arranged in four pseudocycles, 20–22 mm long and 0.8–1 mm in diameter near the base, light brown with longitudinal line. The space between cycles of marginal and labial tentacles dark brown coloured. Labial tentacles 56, about 07 mm long, brown, directive labial present, arrangement

of marginal tentacles 3412.3412.3412... and labial tentacles (2)313.2123.2123.... Oral disk 16 mm wide, stomodeum 10 mm long, dark brown, siphonoglyph wide and rather short with 8 mesenteries attached, hyposulcus 3 mm long with short hemisulci 1 mm long. Free parts of directive mesenteries without mesenterial filament. Second protomesenteries almost reach aboral pole, fertile, bearing ciliated tract with bundle of craspedonemes. Third protomesenteries sterile, longer than B1, with craspedonemes. M and m-metamesenteries long, fertile; M1 and M2 reach 3/4 of total body length and M1 longer than M2, with bundle of craspedonemes; B and b-mesenteries, B twice longer than b.

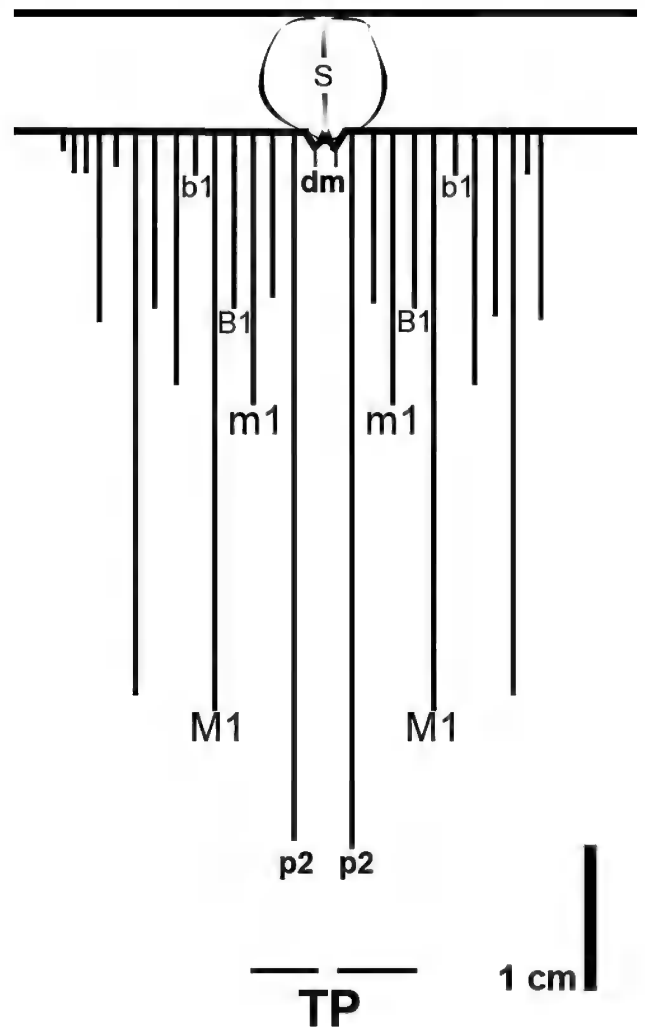


**Figure 11.** Holotype specimen of *Ceriantheopsis zealandiaensis* sp. nov., NIWA 87139. (A) Whole specimen; (B) detail of syphonoglyph.

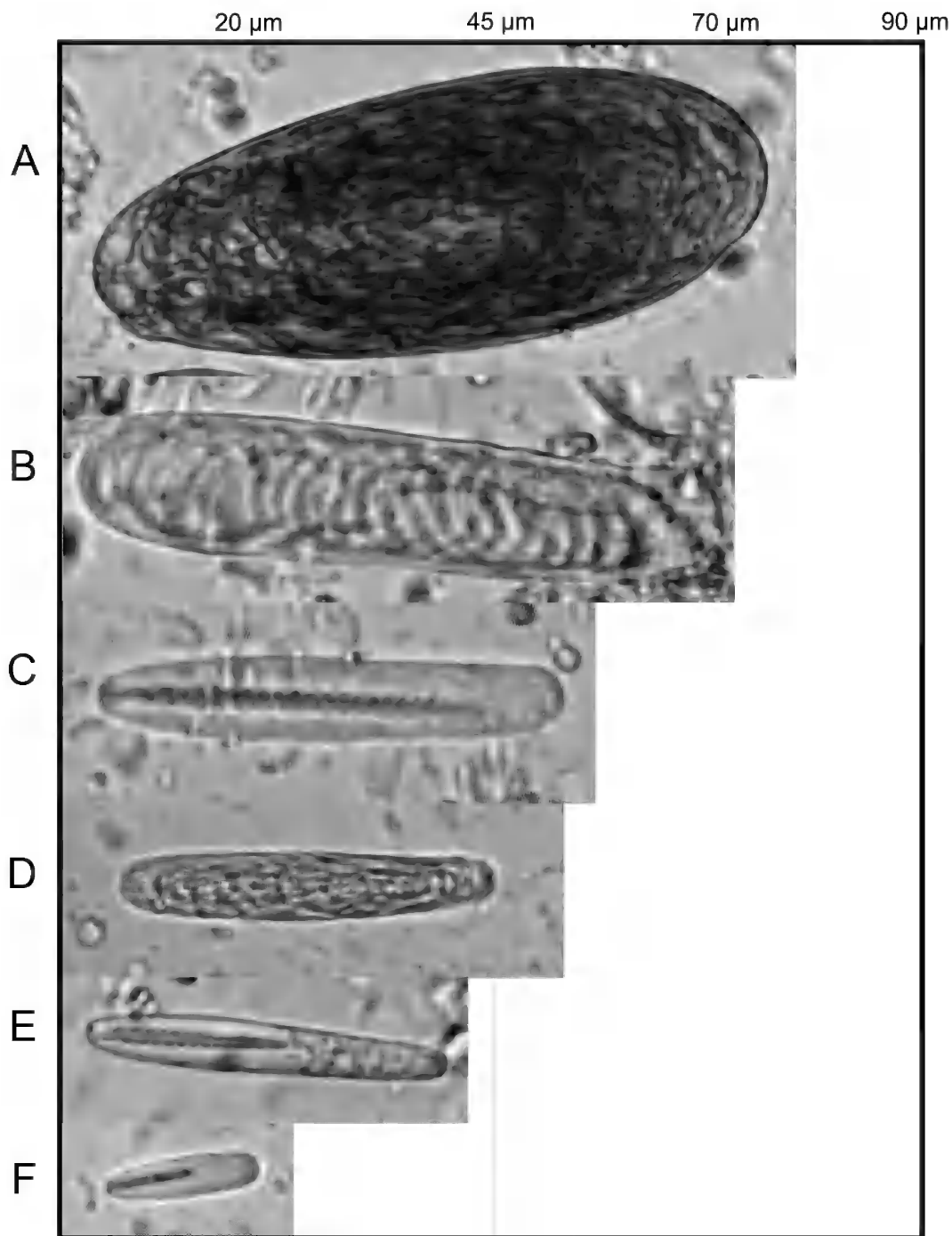
**Remarks.** This species is only known from two specimens collected from a rock wall habitat in Fiordland at scuba diving depths. Environmental conditions in the fjords create unique conditions in the shallow sub-tidal zone, just below the low-salinity layer, making it similar to deep-sea habitats; hence many deep sea dwelling and ancient species can be found at a much shallower depth in Fiordland than anywhere else in the world (Wing, 2003). Ceriantharia have

**Table 4.** Cnidome of *Ceriantheopsis zealandiaensis* sp. nov. based on two specimens (NIWA 87139; 145027). Mean and range given for each cnida.

| <i>Ceriantheopsis zealandiaensis</i> sp. nov. |                            |                           |
|---|----------------------------|---------------------------|
|   | length (in $\mu\text{m}$ ) | width (in $\mu\text{m}$ ) |
| column  |                            |                           |
| pytechocysts                                  | 71.0 (62.5–76.8)           | 28.2 (22.5–35.2)          |
| holotrich                                     | 70.5 (66.4–73.3)           | 17.2 (16.1–18.9)          |
| atrichs                                       | 26.2 (22.5–32.5)           | 7.8 (6.5–8.4)             |
| b-mastigophores ii                            | 28.4 (26.9–29.8)           | 6.4 (5.6–7.5)             |
| marginal tentacles                            |                            |                           |
| b-mastigophores ii                            | 28.2 (26.5–29.7)           | 6.3 (5.5–7.5)             |
| atrichs                                       | 30.5 (29.2–32.1)           | 8.2 (7.8–8.9)             |
| labial tentacles                              |                            |                           |
| b-mastigophores i                             | 41.2 (37.5–43.5)           | 15.4 (13.9–16.7)          |
| b-mastigophores ii                            | 28.2 (26.5–29.7)           | 6.3 (5.5–7.5)             |
| atrichs                                       | 26.4 (24.1–29.4)           | 6.1 (5.6–6.8)             |
| stomodeum                                     |                            |                           |
| b-mastigophores i                             | 42.8 (38.9–46.5)           | 15.8 (14.6–16.4)          |
| b-mastigophores ii                            | 26.7 (25.7–28.7)           | 6.4 (6.0–7.1)             |
| b-mastigophores iii                           | 13.5 (12.4–14.6)           | 3.8 (3.3–4.2)             |
| atrichs                                       | 28.7 (25.6–30.2)           | 7.8 (6.9–8.3)             |
| mesenteries Type b                            |                            |                           |
| atrichs                                       | 27.8 (25.5–29.2)           | 7.6 (6.7–8.2)             |
| mesenteries Type m                            |                            |                           |
| b-mastigophores ii                            | 25.5 (24.7–27.7)           | 6.2 (5.8–7)               |



**Figure 12.** Graphical representation of the arrangement of mesenteries of *Ceriantheopsis zealandiaensis* sp. nov. Abbreviations: M.C., multiplication chamber; dm, directives; T.P., terminal pore; S, siphonoglyph; B, betamesenteries (convoluted mesentery); M, metamesenteries (double filament); P, protomesenteries.



**Figure 13.** Cnidome of *Ceriantheopsis zealandiaensis* sp. nov. based on two specimens (NIWA 97139, 145027).

been recorded as dominant members of the soft sediment community on the sand slope areas of the rock wall zone in Fiordland (Grange *et al.*, 1981), but their ability to escape from the tube they occupy into the sediment is a reason for loss in most sampling attempts (Stampar *et al.*, 2016). Thus, while image-based records of Ceriantharia by divers and underwater camera systems are numerous, corresponding instances of specimens are rare. The range of this species is very close to that recorded for *Pachycerianthus fiordlandensis* sp. nov. and they are probably sympatric in some localities. Although the anatomy is quite distinct, based solely on external morphology it is quite difficult to discern between the two species. However, like all species

of the genus *Ceriantheopsis*, *C. zealandiaensis* is quite thin and long compared to *Pachycerianthus* and this may give a gross guide in the field. Unlike *Pachycerianthus antarcticus*, *Ceriantheopsis zealandiaensis* does not appear to maintain already fertilized oocytes: although both specimens examined are already fully mature, there is no sign of these in the gastrovascular cavities.

**Distribution.** Fiordland, New Zealand.

**Etymology.** The specific name, *zealandiaensis*, is based on the name of the ancient submerged continent that contains New Zealand, the country where the specimens were collected.



## Order Penicillaria Hartog, 1977

Family Arachnactidae McMurrich, 1910

### Genus *Isarachnanthus* Carlgren, 1924

**Type species.** *Isarachnanthus maderensis* (Johnson, 1861).

**Diagnosis** (*sensu* Carlgren, 1924). Arachnactidae with second couple of protomesenteries long, sterile with acontoids. Directive labial tentacle present. Arrangement of metamesenteries in each quartette M,B,m,b (1,3,2,4), more or less distinct.

**Distribution.** This genus is distributed worldwide.

### *Isarachnanthus bandanensis* Carlgren, 1924

*Isarachnanthus bandanensis* Carlgren, 1924: 187–190, 195; Cutress, 1977: 145; den Hartog, 1977: 235; Cutress & Arneson, 1987: 54, 56–58; den Hartog, 1997: 352; Stampar *et al.*, 2012: 1–2, 5–9.

**Specimen examined.** AM G18865, South end of Casuarina Beach, Lizard Island, Queensland, Australia (near rock on rubble reef), 14.6811°S 145.4470°E (xii/1974), low tide.

**Remarks.** This is a nocturnal species, so observing individuals of it requires a specific approach and opportunities for this are limited in many locations. The specimen examined is not complete and is a young individual with no gonads, but it is possible to verify it has a well-formed mesentery. Carlgren (1924) described the species based on specimens from the Banda Islands, Indonesia. From this text, the diagram of the mesenteries, part of the cnidome and the tentacle organization match the specimen examined here, however there are also similarities to *Isarachnanthus panamensis* Carlgren, 1924 which need to be resolved through comparison of material from the type locality of both species. Additionally, there is a need for a review of the genus, especially with the use of molecular data, to verify the consistency of Pacific Ocean species.

**Distribution.** Australia, French Polynesia, Hawaii, and Indonesia, depth: shallow waters.

## Discussion

The Tasman Sea and adjacent areas are relatively well studied for several invertebrate groups, especially Crustaceans and Polychaeta (Glasby & Alvarez, 1999; Williams *et al.*, 2010; Przeslawski *et al.*, 2011). However, some taxa remain poorly known, including a large part of the Cnidaria. One of the cnidarian clades with the lowest number of studies in the region is the subclass Ceriantharia, which has been the focus of only three specific studies in the last 120 years as outlined below.

The first study addressing this group was by Haddon & Shackleton (1893) describing a shallow water species for the northwest region of Australia, *Pachycerianthus nobilis* (as *Cerianthus nobilis*). The present study presents some new data to complement the original description of this species and allow better comparison to other species. Accordingly, it has been possible to validate the status of the species in relation to the others described from the region. Apparently,

*P. nobilis* is a warm water species and tolerates some sub-tropical (mild-cold) waters in southern Queensland.

More than forty years after this first study, Carlgren (1937) described *Arachnanthus australiae* from Queensland, Australia, in the family Arachnactidae. The description is very detailed, especially in relation to generic characters. A specimen of this family examined in the present study is clearly not this species of *Arachnanthus* but matches generic characters of *Isarachnanthus*. The morphology of this specimen corresponds with the *Isarachnanthus bandanensis*, which has been described for Indonesia and this new record represents a range extension consistent with the known distribution of the species.

After a further long interval of almost 60 years, Carter (1995) described two species from Port Jackson (Sydney), New South Wales, Australia. In the current study it became evident that the characters used for differentiation of these two species are not consistent and they should be synonymized, with *P. delwynae* taking precedence.

Also, during the current study, as a result of specimens largely obtained during an environmental impact assessment of the expansion of Sydney Airport in Botany Bay (Wilson *et al.*, 1998), it was possible to recognize a new species of Ceriantharia of very small size, described here as *Ceriantheopsis microbotanica*. These specimens are so small that they were initially identified as members of Actiniaria (family Edwardsiidae). In fact, *P. microbotanica* is associated with samples of, and apparently lives among specimens of, *Edwardsia* sp., although they are slightly larger and have all the morphological characters of Ceriantharia. Therefore, this is the third species of Ceriantharia that inhabits the area between south central New South Wales to southern Queensland along with *Pachycerianthus nobilis* and *P. delwynae*.

Knowledge of New Zealand and Antarctic Ceriantharia was even more limited than reported above for Australia, with no preceding taxonomic study providing anatomical descriptions. Three new species are described in the present study for this area. The species *Pachycerianthus fiordlandensis* and *Ceriantheopsis zealandiaensis* are representatives of rather shallow water taxa occurring in some zones of fiords. *Ceriantheopsis zealandiaensis* and *C. microbotanica* are the first records of the genus in the Pacific region. Unlike the Arctic Ocean, for which some species of Ceriantharia are reported (e.g., *Pachycerianthus borealis*) (Shepard *et al.*, 1986), the Antarctic region has had no described species until now. Therefore, the description of *Pachycerianthus antarcticus* is important for discussions of biogeography. This species is also noteworthy because of the type of sediment in which these organisms live. The construction of the tube in Ceriantharia is a complex process (eg Stampar *et al.*, 2015), and in thicker and rocky sediments particularly difficult. Future studies on these species may provide new insights into the behavior and process of tube construction.

## Morphological characters of new species

Although species are compared in the tables (Tab. 5 and 6) with detailed references, here we highlight diagnostic characteristics for each of them compared to species with close biogeographic affinities. For *Pachycerianthus*, within the area of the South Pacific and Southern Oceans, there are

**Table 5.** Comparison of anatomical features of species of *Pachycerianthus*. (? = no data or uncertain). See text for discussion.

| species                  | directive mesenteries length | directive labial tentacle | M-mesentery (M1) length  | M-mesentery (M2) length | M-mesentery (m1) length | M-mesentery (m2) length | mesenteries attached to siphonoglyph | siphonoglyph shape | no. of marginal tentacles | occurrence area                                 | references   |
|--------------------------|------------------------------|---------------------------|--------------------------|-------------------------|-------------------------|-------------------------|--------------------------------------|--------------------|---------------------------|---|--|
| <i>P. fiordlandensis</i> | < stomodeum                  | present                   | almost reach aboral pore | M-1                     | 4/5 of M1               | 2/3 of M1               | 6                                    | narrow             | 88                        | New Zealand                                     | this Study   |
| <i>P. antarcticus</i>    | < stomodeum                  | absent                    | almost reach aboral pore | longer than M-1         | 2/3 of M1               | 2/3 of M1               | 6                                    | narrow             | 20–33                     | Antarctic Ocean                                 | this Study   |
| <i>P. aestuari</i>       | > stomodeum                  | ?                         | reach aboral pore        | M-1                     | 1/5 of M-1              | = m-1                   | 16                                   | wide               | 30–34                     | USA (Pacific Coast)                             | Torrey & Kleeberg 1909   |
| <i>P. benedeni</i>       | < stomodeum                  | ?                         | reach aboral pore        | ?                       | ?                       | ?                       | 6?                                   | wide?              | ~125                      | Japan   | Role, 1904   |
| <i>P. borealis</i>       | > stomodeum                  | ?                         | reach aboral pore        | = M-1                   | 3/4 of M-1              | ~1/3 of M-1             | 8                                    | wide               | 139–155                   | Canada, USA (North Atlantic)                    | Kingsley, 1904   |
| <i>P. curacaoensis</i>   | > stomodeum                  | absent                    | reach aboral pore        | 1/2 of M-1              | 1/4 of M-1              | 2/3 of m-1              | 4                                    | short and narrow   | 74–105                    | Caribbean Sea (Curaçao)                         | den Hartog, 1977   |
| <i>P. delwynae</i>       | > stomodeum                  | present                   | almost reach aboral pore | longer than M-1         | 1/3 of M-1              | 1/2 of M-1              | 6                                    | narrow             | 89–114                    | Australia                                       | Carter, 1995   |
| <i>P. dahrni</i>         | ?                            |                           | half column              | > M-1                   | ?                       | ?                       | ?                                    | ?                  | ~160                      | Mediterranean                                   | van Beneden, 19;   |
| <i>P. fimbriatus</i>     | > stomodeum                  | present                   | reach aboral pore        | 3/4 of M-1              | 1/3 of M-1              | 1/3 of M-1              | 8                                    | wide and long      | <60                       | Pacific (Canada-USA, Indonesia- Malaysia)       | McMurrich, 1910<br>Arai, 1965  |
| <i>P. insignis</i>       | < stomodeum                  | present                   | almost reach aboral pore | M-1                     | M-1                     | M-2                     | 8                                    | ?                  | ~100                      | Gulf of California-Mexico                       | Carlgren, 1951   |
| <i>P. johnsoni</i>       | < stomodeum                  | ?                         | reach aboral pore        | 3/4 of M-1              | 3/4 of M-1              | 1/2 of M-1              | 8                                    | wide               | ~108                      | USA (Pacific Coast)                             | Torrey & Kleeberg 1909   |
| <i>P. magnus</i>         | > stomodeum                  | present                   | almost reach aboral pore | 3/4 of M-1              | 1/3 of M-1              | 1/2 of M-1              | 6                                    | short and narrow   | ~120                      | Japan, China                                    | Uchida, 1979;  |
| <i>P. maua</i>           | < stomodeum                  | absent                    | reach aboral pore        | 1/4 of M-1?             | 1/3 of M-1?             | 1/3 of M-1?             | 6                                    | narrow             | ~150                      | Red Sea, Gulf of Aden, Tanzania                 | Stampar <i>et al.</i> , 2010<br>Carlgren, 1900, 1910<br>Carter, 1995 |
| <i>P. monostichus</i>    | > stomodeum                  | present                   | reach aboral pore        | M-1                     | 1/2 of M-1              | m-1                     | 8                                    | narrow and long    | ~47                       | Indonesia                                       | McMurrich, 1910  |
| <i>P. multiplicatus</i>  | > stomodeum                  | absent                    | reach aboral pore        | = M-1                   | 1/3 of M-1              | 1/3 of M-1              | 6                                    | narrow             | 175                       | North Sea                                       | Carlgren, 1912;  |
| <i>P. nobilis</i>        | > stomodeum                  | present                   | half column              | 3/4 of M-1              | 1/3 of M-1              | 1/4 of M-1              | 8                                    | wide               | 80–170                    | Australia                                       | Haddon & Shackleton, 1893  |
| <i>P. schlenzoe</i>      | > stomodeum                  | present                   | reach aboral pore        | 3/4 of M-1              | 1/2 of M-1              | 1/3 of M-1              | 6                                    | long and narrow    | 60–85                     | Brazil  | Stampar <i>et al.</i> , 2010   |
| <i>P. solitarius</i>     | > stomodeum                  | present                   | reach aboral pore        | M-1                     | 1/4 of M-1              | 1/5 of M-1              | 6                                    | narrow             | ~64                       | Mediterranean, Black Sea, Aegean Sea, Atlantic. | van Beneden, 19;   |

**Table 6.** Comparison of anatomical features of species of *Ceriantheopsis*. See text for discussion

|  | <i>C. americana</i>   | <i>C. nikitai</i>  | <i>C. austroafricana</i>                                       | <i>C. lineata</i>              | <i>C. microbotanica</i> sp. nov. | <i>C. zealandiensis</i> sp. nov. |
|--|---|--|--|--------------------------------|----------------------------------|----------------------------------|
| marginal tentacles   | up to 100–120   | up to 70   | up to 70   | up to 60                       | 20–38                            | up to 70                         |
| directive labial tentacle                                      | present   | present  | present  | absent                         | present                          | present                          |
| arrangement of labial tentacles                                | (2)413.4232.4312*<br>(4)413.4231.4312.4312  | (3)423.4232.4312.4312  | (2)313.4343.4324.3124  | 4231.4231.4231.4231            | (2)131.3212.3212                 | (2)313.2123.2123                 |
| actinopharynx  | 1/12–1/8 of gastric cavity  | 1/5–1/4 of gastric cavity  | 1/10–1/8 of gastric cavity                                     | 1/6–1/5 of gastric cavity      | 1/7–1/6 of gastric cavity        | 1/7–1/6 of gastric cavity        |
| oral disc  | 0.7–1.0 cm  | c. 0.6–0.7 cm  | wide, c. 1.5 cm in preserved                                   | 1.0–1.5 cm in preserved        | 0.3–0.4 cm                       | 1–2 cm                           |
| siphonoglyph   | narrow, 4 mesenteries attached  | wide, 4 mesenteries attached   | wide, 4 mesenteries attached                                   | narrow, 2 mesenteries attached | narrow, 2 mesenteries attached   | wide, 8 mesenteries attached     |
| directive mesenteries  | < actinopharynx   | ~ actinopharynx  | ~ actinopharynx  | < actinopharynx                | < actinopharynx                  | < actinopharynx                  |
| P2   | to aboral pole  | to aboral pole   | to aboral pole   | almost to aboral pole          | almost to aboral pole            | almost to aboral pole            |
| P3   | = B   | = B  | = B  | = B                            | > B                              | < B                              |
| M  | >> B  | < 2B   | > B  | ≥ B                            | >> B                             | > B                              |
| M3   | ≤ M2  | > M2   | ≤ M2   | < half M2                      | almost = B2                      | < M2                             |
| cnido-glandular tract at fertile mesenteries of first quartets | present   | not present  | present  | present                        | present, very small              | present                          |
| craspedion tract at fertile mesenteries                        | 6/7–8/9   | 3/5  | 6/7  | c. 6/7–8/9                     | 3/5                              | 8/9                              |
| cnido-glandular tract at B                                     | << b  | = b  | < b  | < b                            | = b, very short                  | = b                              |
| craspedonemes of craspedion at fertile mesenteries             | sometimes present   | absent   | absent   | absent                         | absent                           | absent                           |
| references   | McMurrich, 1910; Carlgren, 1912; Molodtsova <i>et al.</i> , 2011, Stampar <i>et al.</i> , 2016b | Molodtsova, 2001; Molodtsova <i>et al.</i> , 2011, Stampar <i>et al.</i> , 2016b | Molodtsova <i>et al.</i> , 2011, Stampar <i>et al.</i> , 2016b | Stampar <i>et al.</i> , 2016b  | this study                       | this study                       |

four species, including the two new species described in this study: *P. antarcticus*, *P. delwynae*, *P. fiordlandensis* and *P. nobilis*. Of these, the easiest to discern is *P. antarcticus*, as this is the only species in which the oral tentacles do not include a directive tentacle. The most obvious differences among the remaining species are related to the organization of the mesenteries. *Pachycerianthus nobilis* has relatively short M1 mesenteries, reaching only half of the gastrovascular cavity whereas the other two species, *P. delwynae* and *P. fiordlandensis*, have M1 mesenteries reaching almost to the aboral pore. The two remaining species can be differentiated by the following mesenterial couples—*P. fiordlandensis* has M2 with the same length as M1 and m2 with 2/3 of the length of M1; conversely *P. delwynae* has M2 longer than M1 and m2 shorter than 1/2 of the length of M1. For *Ceriantheopsis*, there is no previous record of the genus in the Pacific Ocean. However, unpublished data indicate the occurrence of species in Japan and surrounding areas (SNS, personal observation). The two species described in this study can be easily identified by the difference in the number of mesenteries connected to the siphonoglyph area, *Ceriantheopsis zealandiaensis* has 8 mesenteries connected to the siphonoglyph area, whereas *C. microbotanica* has only 2.

Although ecological inferences are important, this information is almost totally unknown for these species. Further studies, especially on the life cycle, are essential for the better understanding and conservation of these species and others yet to be scientifically documented but occurring commonly, throughout the Indo-Pacific region.

**ACKNOWLEDGEMENTS.** This work was partly funded by FAPESP (grants 2015/24408-4, 2015/21007-9, 2016/04962-0 and 2016/50389-0), CNPq (grants 404121/2016-0 and 301293/2019-8) and Acordo CAPES/CNPq—PROTAX II (grants 88882.156878/2016-01). Study of the cnidarian collections of the Australian Museum was supported by an Australian Museum Research Institute (AMRI) Visiting Collection Fellowship for the first author. We gratefully acknowledge the wonderful photographs taken of Ceriantharia in the wild by Tony Strazzani, Malcolm P. Francis and Chris Woods, and those on deck by Stefano Schiaparelli, and the people that were able to collect these elusive creatures. Specimens and data provided from the NIWA Invertebrate Collection were collected on various research surveys including by Mike Page on a New Zealand Department of Conservation (DOC) survey in Fiordland with thanks to DOC and the Fiordland Marine Guardians; TAN0906: Ocean Survey 20/20 Bay of Islands Coastal Biodiversity, Sediment and Seabed Habitat Project, funded and owned by Land Information New Zealand (LINZ); TAN0802: research funded by the New Zealand Government under the New Zealand International Polar Year Census of Antarctic Marine Life Project (Phase 1: So001IPY; Phase 2: IPY2007-01) with project governance provided by the former Ministry of Fisheries (MFish) Science Team and the Ocean Survey 20/20 CAML Advisory Group (LINZ, MFish, Antarctica New Zealand, Ministry of Foreign Affairs and Trade, and NIWA); TAN0402: A biodiversity survey of the western Ross Sea and Balleny Islands in 2004 undertaken by NIWA and funded by MFish. We are also grateful to the Drs Marymegan Daly and James Reimer who provided constructive comments on an earlier version of this manuscript.

## References

- Arai, M. N. 1965. A new species of *Pachycerianthus*, with discussion of the genus and an appended glossary. *Pacific Science* 19: 205–218.
- Atlas of Living Australia. [Accessed 10 August 2019]  
<https://www.ala.org.au/>
- Butler, A. J., T. Rees, P. Beesley, and N. J. Bax. 2010. Marine Biodiversity in the Australian Region. *PLoS ONE* 5(8): e11831.  
<https://doi.org/10.1371/journal.pone.0011831>
- Cairns, S. D., L. A. Gerhswin, F. Brook, P. R. Pugh, E. W. Dawson, V. Ocaña, W. Vervoort, G. Williams, J. Watson, D. M. Opresko, P. Schuchert, P. M. Hine, D. P. Gordon, H. J. Campbell, A. J. Wright, J. A. Sánchez, and D. G. Fautin. 2009. Phylum Cnidaria; corals, medusae, hydroids, Myxozoa. Chapter 4. In *New Zealand Inventory of Biodiversity. Volume 1. Kingdom Animalia: Radiata, Lophotrochozoa, Deuterostomia*, ed. D.P. Gordon, pp. 59–101. Canterbury University Press, Christchurch, New Zealand.
- Carlgrén, O. 1893. Studien über nordische Actinien. *Kungliga Svenska Vetenskapsakademiens Handlingar* 25: 1–148.
- Carlgrén, O. 1900. Ostafrikanische Actinien. Gesammelt von Herrn Dr. F. Stuhlmann 1888 und 1889. *Mittheilungen aus dem Naturhistorischen Museum* 17: 21–144.
- Carlgrén, O. 1912. Ceriantharia. *Danish Ingolf-Expedition* 5: 1–79.
- Carlgrén, O. 1924. Papers from Dr. Th. Mortensen's Pacific expedition 1914–16. XVI. Ceriantharia. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 75: 169–195.
- Carlgrén, O. 1937. Ceriantharia and Zoantharia. *Scientific Reports of the Great Barrier Reef Expedition 1928–29* 5: 177–207.
- Carlgrén, O. 1951. The actinian fauna of the Gulf of California. *Proceedings of the United States National Museum* 101: 415–449.  
<https://doi.org/10.5479/si.00963801.101-3282.415>
- Carter, S. 1995. *Pachycerianthus* (Anthozoa: Cerianthidea), two newly described species from Port Jackson, Australia. *Records of the Australian Museum* 47(1): 1–6.  
<https://doi.org/10.3853/j.0067-1975.47.1995.3>
- Cutress, C. E. 1977. Corallimorpharia, Actiniaria, Ceriantharia. In *Reef and Shore Fauna of Hawaii*, eds D. M. Devaney and L. G. Eldredge, pp. 130–147. Honolulu: Bishop Museum Press.
- Cutress, C. E., and C. A. Arneson. 1987. Sea anemones of Enewetak Atoll. In *The Natural History of Enewetak Atoll*, ed. D. M. Devaney, E. S. Reese, B. L. Burch, and P. Helfrich, pp. 53–62. Office of Scientific and Technical Information, US Department of Energy, Honolulu.
- Darling, J. A., A. R. Reitzel, P. M. Burton, M. E. Mazza, J. F. Ryan, J. C. Sullivan, and J. R. Finnerty. 2005. Rising starlet: the starlet sea anemone, *Nematostella vectensis*. *Bioessays* 27(2): 211–221.  
<https://doi.org/10.1002/bies.20181>
- den Hartog, J. C. 1977. Descriptions of two new Ceriantharia from the Caribbean region, *Pachycerianthus curancaensis* n.sp. and *Arachnanthus nocturnus* n.sp. with a discussion of the cnidom and of the classification of the Ceriantharia. *Zoologische Mededelingen* 51: 211–242.
- den Hartog, J. C. 1997. Sea anemones. In *A guide to the seashores of Eastern Africa*, ed. M. D. Richmond, pp. 134–139. Sida/ Department for Research Cooperation, SAREC.
- Doak, W. 1971. *Beneath New Zealand Seas*. Auckland: A. H. & A. W. Reed.
- England, K. W. 1991. Nematocysts of sea anemones (Actiniaria, Ceriantharia and Corallimorpharia: Cnidaria): nomenclature. *Hydrobiologia* 216/217: 691–697.  
<https://doi.org/10.1007/BF00026532>
- Gage, J. D., and B. J. Bett. 2005. Deep-sea benthic sampling. In *Methods for the Study of the Marine Benthos*, ed. A. Eleftheriou, pp. 273–325. Oxford: Blackwell.  
<https://doi.org/10.1002/9780470995129.ch7>

- Glasby, C. J., and B. Alvarez. 1999. Distribution patterns and biogeographic analysis of Austral Polychaeta (Annelida). *Journal of Biogeography* 26(3): 507–533.  
<https://doi.org/10.1046/j.1365-2699.1999.00297.x>
- Grange, K. R., and F. J. Brook. 2010. Class Anthozoa. In *New Zealand Coastal Marine Invertebrates volume 1*, ed. S. de C. Cook, pp. 139–177. Christchurch: Canterbury University Press.
- Griffiths, H. J. 2010. Antarctic marine biodiversity—what do we know about the distribution of life in the Southern Ocean? *PLoS One* 5(8): e11683.  
<https://doi.org/10.1371/journal.pone.0011683>
- Haddon, A. C., and A. M. Shackleton. 1893. Description of some new species of Actiniaria from Torres Straits. *Scientific Proceedings of the Royal Dublin Society* 8: 116–131.
- Haddon, A. C. 1898. The Actiniaria of Torres Straits. *Scientific Transactions of the Royal Dublin Society* 6: 393–520.
- He, S., J. A. Grasis, M. L. Nicotra, C. E. Juliano, and C. E. Schnitzler. 2019. Cnidofest 2018: the future is bright for cnidarian research. *EvoDevo* 10: 20.  
<https://doi.org/10.1186/s13227-019-0134-5>
- Hutchings, P. A. 1992. *Biology—A survey of Elizabeth and Middleton Reefs, South Pacific*. Canberra: Australian National Parks and Wildlife.
- Kelly, E., and B. F. Keegan. 2000. Case 3111. *Pachycerianthus* Roule, 1904 (Cnidaria, Anthozoa): proposed designation of *P. multiplicatus* Carlgren, 1912 as the type species. *Bulletin of Zoological Nomenclature* 57: 11–13.  
<https://doi.org/10.5962/bhl.part.20659>
- Kennedy, B. R., K. Cantwell, M. Malik, C. Kelley, J. Potter, K. Elliott, E. Lobecker, L. McKenna Gray, D. Sowers, S. France, and S. Auscavitch. 2019. The unknown and the unexplored: insights into the Pacific deep-sea following NOAA CAPSTONE expeditions. *Frontiers in Marine Science* 6: 480.  
<https://doi.org/10.3389/fmars.2019.00480>
- Kingsley, J. S. 1904. A description of *Cerianthus borealis* Verrill. *Tufts College Studies* 1: 345–361.
- McMurrich, J. P. 1910. Actiniaria of the Siboga expedition, part I. Ceriantharia. *Siboga-Expedition Monographes* 10: 1–48.
- Molodtsova, T. N. 2000. Fauna ceriantariy atlanticheskogo okeana I sostav roda *Cerianthus* mirovoy fauny. Aftoreferat na soiskanie uchenoy stepeni kandidata biologicheskikh nauk. Moscow: Dialog-MGU.
- Molodtsova, T. N. 2001. Cerianthids (Anthozoa, Cnidaria) of the region of Bengual upwelling I. *Ceriantheopsis nikitai* n.sp. *Zoologicheskii Zhurnal* 80: 773–780 (in Russian, translated to Portuguese).
- Molodtsova, T. N. 2007. Tube anemones (Ceriantharia Anthozoa) of New Caledonia. Compendium of marine species of New Caledonia. *Documents scientifiques et techniques, IRD Nouméa, II7* (volume spécial, deuxième édition), 133.
- Molodtsova, T. N., C. L. Griffiths, and F. H. Acuña. 2011. A new species of shallow-water cerianthid (Cnidaria: Anthozoa) from South Africa, with remarks on the genus *Ceriantheopsis*. *African Natural History* 7: 1–8.
- Nyholm, K.-G. 1943. Zur Entwicklung und Entwicklungsbiologie der Ceriantharien und Aktinien. *Zoologiska Bidrag från Uppsala* 22: 87–248.
- Pax, F. 1910. Studien an westindischen Actinien. *Zoologische Jahrbucher. Abteilung für allgemeine zoologie und physiologie der tiere suppl* 11: 157–330.
- Przeslawski, R., A. Williams, S. L. Nichol, M. G. Hughes, T. J. Anderson, and F. Althaus. 2011. Biogeography of the Lord Howe rise region, Tasman Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 58(7–8): 959–969.  
<https://doi.org/10.1016/j.dsr2.2010.10.051>
- Roule, L. 1904. Note preliminaire sur quelques formes nouvelles de cerianthaires. *Comptes Rendus de l'Association Française pour l'Avancement des Sciences* 32: 791–793.
- Shepard, A. N., R. B. Theroux, R. A. Cooper, and J. R. Uzzmann. 1986. Ecology of Ceriantharia (Coelenterata, Anthozoa) of the northwest Atlantic from Cape Hatteras to Nova Scotia. *Fishery Bulletin* 84: 625–646.
- Stampar, S. N., C. C. Emig, A. C. Morandini, G. Kodja, A. P. Balboni, and F. L. Silveira. 2010. Is there any risk in a symbiotic species associating with an endangered one? A case of a phoronid worm growing on a *Ceriantheomorphe* tube. *Cahiers de Biologie Marine* 51(2): 205–211.  
<https://doi.org/10.21411/CBM.A4FB77E7>
- Stampar, S. N., M. M. Maronna, M. J. A. Vermeij, F. L. Silveira, and A. C. Morandini. 2012. Evolutionary diversification of banded tube-dwelling anemones (Cnidaria; Ceriantharia; *Isarachnanthus*) in the Atlantic Ocean. *PLoS ONE* 7: e4109.  
<https://doi.org/10.1371/journal.pone.0041091>
- Stampar, S. N., M. M. Maronna, M. V. Kitahara, J. D. Reimer, and A. C. Morandini. 2014. Fast-evolving mitochondrial DNA in Ceriantharia: a reflection of Hexacorallia paraphyly? *PLoS ONE* 9: e86612.  
<https://doi.org/10.1371/journal.pone.0086612>
- Stampar, S. N., A. C. Morandini, and F. L. Silveira. 2014. A new species of *Pachycerianthus* (Cnidaria, Anthozoa, Ceriantharia) from tropical southwestern Atlantic. *Zootaxa* 3827: 343–354.  
<https://doi.org/10.11646/zootaxa.3827.3.4>
- Stampar, S. N., J. S. Beneti, F. H. Acuña, and A. C. Morandini. 2015. Ultrastructure and tube formation in Ceriantharia (Cnidaria, Anthozoa). *Zoologischer Anzeiger* 254: 67–71.  
<https://doi.org/10.1016/j.jcz.2014.11.004>
- Stampar, S. N., M. M. Maronna, M. V. Kitahara, J. D. Reimer, J. S. Beneti, and A. C. Morandini. 2016a. Ceriantharia in current systematics: life cycles, morphology and genetics. In *The Cnidaria, Past, Present and Future: The world of Medusa and her sisters*, ed. S. Goffredo and Z. Dubinsky, pp. 61–72. Cham: Springer International Publishing.  
[https://doi.org/10.1007/978-3-319-31305-4\\_5](https://doi.org/10.1007/978-3-319-31305-4_5)
- Stampar, S. N., F. Scarabino, G. Pastorino, and A. C. Morandini. 2016b. A new species of tube-dwelling anemone (Cnidaria, Anthozoa, Ceriantharia, *Ceriantheopsis*) from the warm temperate South-western Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 96(7): 1475–1481.  
<https://doi.org/10.1017/S0025315415001745>
- Torrey, H. B., and F. L. Kleeberger. 1909. Contributions from the laboratory of the Marine Biological Association of San Diego. XXVII. Three species of *Cerianthus* from southern California. *University of California Publications in Zoology* 6: 115–125.
- Uchida, H. 1979. Cerianthids (Anthozoa, Coelenterata) from Kii Region, Middle Japan. *Memoirs of the National Science Museum* 12: 185–199.
- van Beneden, E. 1897. Les Anthozoaires de la “Plankton-Expedition” (Die Anthozoen der Plankton-Expedition). *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung* 2K: 1–222.
- van Beneden, E. 1924. Travaux posthumes d’Edouard van Beneden sur les cérianthaires collationnés par Paul Cerfontaine. *Archives de Biologie hors serie*: 1–242.
- Verrill, A. E. 1864. Revision of the “Polypi” of the eastern coast of the United States. *Memoirs of the Boston Society of Natural History* 1: 1–45.  
<https://doi.org/10.5962/bhl.title.78052>
- Wallace, C. C., and A. L. Crowther. 2019. Hexacorals 1: Sea anemones and anemone-like animals (Actinaria, Zoantharia, Corallimorpharia, Ceriantharia and Antipatharia). In *The Great Barrier Reef: Biology, Environment and Management*, ed. P. Hutchings, M. Kingsford, and O. Hoegh-Guldberg, pp. 257–266. Boca Raton: CRC Press.

- Williams, A., F. Althaus, P. K. Dunstan, G. C. Poore, N. J. Bax, R. J. Kloser, and F. R. McEnnulty. 2010. Scales of habitat heterogeneity and megabenthos biodiversity on an extensive Australian continental margin (100–1100 m depths). *Marine Ecology* 31(1): 222–236.  
<https://doi.org/10.1111/j.1439-0485.2009.00355.x>
- Wilson, G. 1998. *A Post-impact Monitoring Study in Subtidal Areas Dredged for the Third Parallel Runway in Botany Bay. Report prepared for the Federal Airports Corporation*. Sydney: Australian Museum Business Services.
- Wing, S. 2003. Fiordland. Chapter 30. In *The Living Reef: The ecology of New Zealand's Rocky Reefs*, ed. N. Andrew and M. Francis, pp. 238–247. Nelson: Craig Potton Publishing.
- Wing, S. 2008. *Subtidal Invertebrates of New Zealand a Diver's Guide*. Christchurch: Canterbury University Press.







# INSTRUCTIONS TO AUTHORS

Manuscripts must be submitted to the Editor. All manuscripts are refereed externally. Members of the Editorial Committee oversee the peer-review process and establish publication standards.

Only those manuscripts that meet the following requirements will be considered for publication.

Submit manuscripts and images separately and electronically; images should be high resolution TIFF or PSD (see below). Attach one summary file giving: the title; the name, address, email and ORCID of each author; the author responsible for checking proofs; a suggested running-head of less than 40 character-spaces; and the number of figures, tables and appendices. Manuscripts must be complete when submitted.

Tables and figures should be numbered and referred to in numerical order in the text. Authors should avoid excessive layout or textual embellishments.

All copy is manipulated within a Windows (not Mac) environment using Microsoft and Adobe software. Maps should be submitted as high resolution TIFF or PSD.

Manuscripts should be prepared using recent issues as a guide. There should be a title (series titles should not be used), author(s) with their institutional addresses, an abstract (should be intelligible by itself, informative not indicative), introduction (should open with a few lines for general, non-specialist readers), materials and methods, results (usually subdivided with primary, secondary and rarely tertiary-level headings), discussion, acknowledgments and references. If appropriate, an appendix may be added after references.

In the titles of zoological works the higher classification of the group dealt with should be indicated. Except for common abbreviations, definitions should be given in the materials and methods section. Sentences should not begin with abbreviations or numerals; generic names should not be abbreviated if at the beginning of a sentence. Metric units must be used except when citing original specimen data. It is desirable to include geo-spatial coordinates; when reference is made to them, authors must ensure that their format precludes ambiguity, in particular, avoid formats that confuse arcminutes and arcseconds.

Label and specimen data should, as a minimum requirement, indicate where specimens are deposited, in addition to locality, date and collector. Original specimen data—especially that of type material—is preferred over interpreted data. If open to interpretation, cite original data between quotation marks or use “[sic]”.

Rules of the International Code of Zoological Nomenclature must be followed; authors must put a very strong case if a Recommendation is not followed. When new taxa are proposed in works having multiple authors, the identity of the author(s) responsible for the new name(s) and for satisfying the criteria of availability, should be made clear in accordance with Recommendations in Chapter XI of the Code. A scientific name with more than two authors is unwieldy and should be avoided. Keys are desirable; they must be dichotomous and not serially indented. Synonymies should be of the short form: taxon author, year, pages and figures. A period and em-dash must separate taxon and author, except in the case of reference to the original description. Proposed type material should be explicitly designated and, unless institutional procedure prohibits it, registered by number in an institutional collection.

Previously published illustrations will generally not be accepted. Colour is acceptable but only where necessary. All images must (a) be rectangular or square and scalable to a width of 83 mm (= one text column) or 172 mm (= both text columns including central gutter) and any depth up to 229 mm (the number of lines in a caption limits depth); (b) have lettering similar to 14 pt, upper case, regular, *sans serif* Helvetica or Arial, in final print; (c) have no unnecessary white or black space; and (d) have vertical or horizontal scale bar(s) with the thickness approximately equal to an upper case 14 pt letter “l”.

Digital images must be presented as TIFF, or as multilayered PSD files suitable for *Adobe Photoshop*. Halftone and colour images must be at a minimum resolution of 300 dpi at final size (at this resolution 2040 pixels = printed-page width = 172 mm) and all labelling must be sharp (with *anti-alias* active). Black and white line images (bitmaps) must be at a minimum resolution of 1200 dpi at final size (at this resolution, 8160 pixels = printed-page width).

When reference is made to figures in the present work use Fig. or Figs, when in another work use fig. or figs; the same case-rule applies to the words *tables*. Figures and tables should be numbered and referred to in numerical order in the text.

Authors should refer to recent issues of the *Records of the Australian Museum* to determine the correct format for listing references and to *The Chicago Manual of Style* to resolve other matters of style. If *EndNote* is used, *Chicago 16th B* output-style closely approaches the required specification. *CrossRef*-minted DOI's are inserted automatically during copyediting (see [crossref.org/SimpleTextQuery/](http://crossref.org/SimpleTextQuery/)); DOI minted by other agencies (e.g., *DataCite*) should be entered by authors.

Certain anthropological manuscripts (both text and images) may deal with culturally sensitive material. Responsibility rests with authors to ensure that approvals from the appropriate person or persons have been obtained prior to submission of the manuscript.

Stratigraphic practice should follow the *International Stratigraphic Guide* (second edition) and *Field Geologist's Guide to Lithostratigraphic Nomenclature in Australia*.

The Editor and Publisher reserve the right to modify manuscripts to improve communication between author and reader. Essential corrections only may be made to final proofs. No corrections can be accepted less than 10 days prior to publication without cost to the author(s). All proofs should be returned as soon as possible.

No duplicates or reprints are printed.

All authors, or the Corresponding Author on their behalf, must sign a *Licence to Publish* when a manuscript is submitted, and certify that the research described has adhered to the Australian Museum's *Guidelines for Research Practice*—or those of their home institution providing they cover the same issues, especially with respect to authorship and acknowledgment. While under consideration, a manuscript may not be submitted elsewhere.

More information and examples are freely available at our website:

<https://doi.org/10.3853/issn.2201-4349>

Editor, *Records of the Australian Museum*

Australian Museum Research Institute

Australian Museum, 1 William Street, Sydney NSW 2010, Australia

[editor@austmus.gov.au](mailto:editor@austmus.gov.au)



Australian Museum Research Institute  
1 William Street, Sydney NSW 2010  
scientific publications freely accessible at  
<https://doi.org/10.3853/issn.2201-4349>  
ISSN 0067-1975 (print) 2201-4349 (online)